GUANA REPORT for 1998

NIGHT LIFE
in the British Virgin Islands

Female *Eleutherodactylus cochranae* following a male
to a nest site during courtship,
Sage Mountain, Tortola (ca. 1.3 x life size)

The Conservation Agency

TCA

Exploration, Education, and Research

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

5 May 1999

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

Dr. Henry Jarecki
10 Timber Trail
Rye, NY 10580

Dear Henry:

Herewith my report of 1998 activities. Two frog papers, the new skink description, and our second lizard physiology paper remain "in press." That is very frustrating; several have been that way now for two years.

Rob Bleiweiss came and collected hummingbirds in the late eighties. Obviously, he was just beginning his work then, and it has taken all this time for him to collect and work up samples from the rest of the Americas. At last, the results: very impressive, cutting edge stuff. Fred continues to get great birds; see also his dragonfly contribution, our first.

In addition to our record ground gecko density, Numi's iguana papers are coming out: one already published, the second in press. It was a complete surprise to find the lizard parasite paper. The author did not know us, but he does now, and we will get him more material.

Mike Ivie's coauthors have overcome his inertia. Keith Philips has published one of his several papers on beetles and Wenhua has gotten hers accepted, in press. Therein is Glipostenoda guana, a pretty little flower beetle -- and lots more.

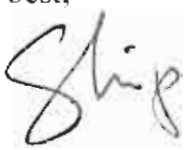
Jean Lodge has a fungus paper submitted: draft follows. I am on the cases of George Proctor, Thorne and Denno, and Jim Ortiz (the spider man) because I do not know what they are doing. At least George has been helped by Numi to complete his MS and I hope has submitted it.

For 1999, we will have several new entomologists working on groups un- or understudied. We plan to try again for our three month lizard physiology

project with Clive and Dawn from HLSCC. We plan a major iguana census and radio-tracking of both iguanas and tortoises.

Did you get a long report from marine biologist Leslie Harris, LACM? She sent a copy to me and one to Lianna, so I assumed Lianna included it in her marine month report to you. I have not seen that yet.

All the best,



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COVER STORY

Eleutherodactylus cochranae is the smallest, scarcest, and least-known of the three BVI piping frogs. It is named for Dr. Doris Cochran, late of the Smithsonian, and a dominant figure in herpetology -- especially frog studies -- in midcentury. In the fifties, she was suspected of smuggling gemstones into the U.S. inside of the bodies of pickled specimens. The story goes that when the authorities got to the specimens, a day or two after Dr. Cochran's arrival in Washington, all were indeed, dissected. Of course, Dr. Cochran said for biological purposes, but it was a lot of work to do in a short time. Some of us do not get around to dissecting our specimens for years.

Anyway, no gems were found.

When Kris and Jeannine published on E cochranae in 1997, they had only sketchy knowledge of courtship. Because these frogs live high up in big trees, they are very hard to study. In 1998 they got lucky and found several accessible nest studies.

E. cochranae does not now occur on Guana, but it does occur in very arid places, given big trees. It must once have occurred on Guana, presumably in the forest on the flat prior to clearing for agriculture. Should we bring them back? Their voice is a high-pitched "wheep," inaudible to many people. They would probably take readily to the big seagrape trees on the flat today.

west indies region

Guana marked blue

ROBERT L. NORTON

The Bahamas archipelago were well canvassed this season. Tony White and a small cadre of dedicated Bahamian birders provided records of birds from Abaco and the Berry Islands in the northwest Bahamas to about as far southeast as one can get, Mayaguana and Great Inagua. They gave us a particularly interesting report where few birders go or report to the rest of us. Between the "book-ends" of the Bahamas, Bruce Hallett, Paul Dean, and Aileen Bainton reported from Grand Bahama, Andros, and New Providence. White, along with the Audubon Naturalist Society, visited Turks and Caicos Islands. Although geographically connected to the Bahamas, the Turks and Caicos are politically connected to Great Britain. Daphne Gemmill reported again from Vieques, Puerto Rico, after a short hiatus. Fred Sibley reported on banded birds and observations from Guana and Anegada islands in the British Virgin Islands, supporting sight records of rarely seen warblers east of Puerto Rico. And Andrew Dobson continues to report from Bermuda on the always fascinating fallouts there.

Weather was unusual, to say the least. For example, at Bermuda August rainfall was 110% above average, while September was 80% above normal. October was relatively quiet with no major fronts producing rain or bird fallout, according to Dobson. November cold fronts sweeping through the northern Bahamas eventually provided some 20 warbler species days and a few sparrow treats. Many of the reports from Bermuda represent the earliest sightings on record for some species. Are birds breeding sooner and leaving sooner? Or were weather patterns a little more favorable this fall for early overshooting and fallout in distant locales? And, finally, Gemmill reports that local residents in Vieques reported woodpeckers to be common, and Antillean Crested Hummingbirds have also appeared to rebound since the ravages of hurricane *Hugo* in 1989.

Abbreviations: BA *(Bahamas)*; BE *(Bermuda)*; BVI *(British Virgin Islands)*; MB salt pans *(Morton Bahamas Ltd. salt pans, Great Inagua, Bahamas)*; PR *(Puerto Rico)*.

SHEARWATER THROUGH TERNS

A moribund Audubon's Shearwater was found at Elbow Beach, BE, Sept. 26. Dobson reports that this is a significant observation, because it is the first record since the species last bred at Bermuda in the 1980s. Brown Booby was nesting at Mayaguana, BA, Oct. 24–29. A single Neotropic Cormorant was noted at Marsh Harbor, Abaco, BA, Oct. 6 for the 2nd record there, and 125 were seen at MB salt pans Oct. 30 at Great Inagua, BA. An Am. Bittern was noted at Grand Bahama for one of the few reports from the Bahamas (BH), and a Least Bittern was noted at new Providance, BA, Oct. 25. A ad. White Ibis was seen at Chub Bay, Berry Is, BA, Nov. 22–23, and a Glossy Ibis was seen at Marsh Harbour, Abaco, Oct. 10. Two Roseate Spoonbills were noted at MB salt pans Oct. 31 (TW et al.).

Greater Flamingos (212) were seen daily at Mayaguana from Oct. 24–29 (AB) moving between Besty Bay and Blackwood Pt. No recent nesting has been confirmed there. On North Caicos, 220 flamingos were counted Nov. 9–11 (TW et al.). At Great Inagua, however, 500+ Greater Flamingos were seen at the salt pans and L. Windsor Oct. 31, where Henry Nixon, senior warden and long time flamingo conservationist, and brother Jimmy Nixon of the Bahamas National Trust, said that this was the 3rd consecutive year that more than 10,000 young birds fledged there. Two decades ago 30,000–40,000 birds represented over half the world's population (Buden 1987)!

The 2nd Greater White-fronted Goose for Bermuda appeared Sept. 20 and stayed until Oct. 11. Always good are reports of West Indian Whistling-Ducks. Two were noted on Andros Oct. 30 (BH). A Wood Duck, very infrequently reported from the Bahamas, was seen at New Providence Oct. 25 (BH), for perhaps the earliest record there. White-cheeked Pintails numbered 15 at New Providence Oct. 25 (BH), and 30 were seen n. of the MB salt pans Oct. 30. A Black Scoter appeared at Spittal Pond, BE, for only the 6th record there.

A Northern Harrier was seen at New Providence Oct. 31 (BH, TW) for one of the few reports from the c. Bahamas. A single Peregrine was reported from Nonsuch Island, BE, Sept. 4, the earliest date by 9 days. Peregrine Falcons may be in danger of being delisted if reports from the Bahamas are the sole criterion. On Oct. 5, four were seen from Hole-in-the-Wall to Bahama Palm Shores, Abaco (TW); one was reported from Grand Bahama Nov. 4 (TW); and one was seen Nov. 11 at North Caicos. That's six in about 40 days.

One Am. Golden-Plover was noted at the airfield at Vieques, PR, Aug. 29 for one of the few reports from that island. Singleton Piping Plovers were seen at Green Tur-

tle Cay, Abaco, Oct. 9, and at Northwest Pt., Providenciales, Caicos Is., Nov. 11 (TW et al.). A single Snowy Plover was found at Pirate's Well, Mayaguana, Oct. 24. A juv. Dunlin was seen at Diamond Farm, New Providence, Nov. 1 (PD), and was subsequently photographed (BH). A Solitary Sandpiper was noted at Guana, BVI, Oct. 10 (FS) for one of the few reports from the smaller islands there.

A Great Black-backed Gull was seen at Grand Bahama Nov. 5 (BH) for one of the few reports from the Bahamas. A Ring-billed Gull Oct. 26 at Mayaguana (AB) may represent only the 2nd record there. A Herring Gull also at Mayaguana Oct. 28 provided probably the first report from that island (Buden 1987). Each was in first fall plumage. As time passes and consistent reporting emerges from the Bahamas, we will probably see reports of the same gull species reported from Florida.

A rare fall report of Com. Tern was noted at L. Cunningham, New Providence, Oct. 25 (BH). It was carefully studied when sitting and flying, with field marks (carpal bar and darkish primaries) noted. Another five were seen some distance away at Mayaguana for 3 days beginning Oct. 27 (TW et al.), and one was at Mangrove Cay, N. Caicos (TW). A Forster's Tern was seen at Grand Bahama Nov. 5 (BH et al.), and two were seen at L. Windsor, Great Inagua, Oct. 30 (TW et al.). A Black Skimmer was noted off Sandy Pt., Abaco, Sept. 1 (CM) for one of few records in the n. Bahamas.

DOVES THROUGH BLACKBIRDS

The always elusive Key West Quail-Doves were evident Oct. 6 at Elbow Cay, Abaco (TW, AB) and at N. Caicos Nov. 9–12 (TW et al.). Two Cuban Parrots were seen near the airfield at Great Inagua Oct. 30 (TW). Six Yellow-billed Cuckoos were seen Oct. 19 at Anegada, BVI (FS), suggesting a temporary migration bottleneck there. Smooth-billed Anis were found to be common near settlements at Mayaguana, where Buden (1987) had not recorded them.

Short-eared Owls may be making a range expansion e. of Puerto Rico into its satellite islands, and e. to the Virgin Islands in the last decade or so. A single bird was noted at Vieques, PR, Aug. 30. St. Thomas also has a record from last decade. A Ruby-throated Hummingbird was noted Oct. 12 and provided one of three records at Bermuda this season. Dobson reports that of the 30 records since 1852, at least 67% (20) have occurred since 1974. A single female Ruby-throated Hummingbird found at Grand Bahama Nov. 5 (BH) furnished one of few recent records from the n. Bahamas.

A West Indian Red-bellied Woodpecker noted daily at Marsh Harbour, Abaco, from Aug. 31–Sept. 1 (CM) was good news, since this species seems to be going through some distribution or abundance fluctuations. A special effort to survey this Regional endemic is warranted. An E. Wood-Pewee was seen Oct. 8 at Coopers Town dump for one of the few records from the n. Bahamas. Bermuda's 6th record of Olive-sided Flycatcher was recorded Sept. 21, the first since 1985. A House Wren at Grand Bahama Nov. 4 was not only unusual, but earlier than previous records (Brudenell-Bruce 1975). One Bank and 20 Cliff swallows were seen at Vieques from Aug. 29–Sept. 1 (DG). Two N. Rough-winged Swallows, another rare passage migrant in the Bahamas, were seen Oct. 10 at Sugarlands Farm, Abaco.

Cuban Crows (30) were noted at N. Caicos Nov. 9–11 (TW). They are persecuted in the Caicos because they are perceived as a threat to subsistence agriculture (Norton 1989). Mowery reports first hearing the distinctive nasal call, then seeing a **Fish Crow** at Marsh Harbour, Abaco, Aug. 31. This is a remarkable sighting because it strongly suggests that the first record for the West Indies at West End, Grand Bahama, from February 13–15,1997 (m.ob.) has survived, and may be the same bird now found in Abaco, only 140 mi due east as the crow flies.

Red-eyed Vireos have been an annual occurrence at Guana, BVI, whence Sibley has netted/banded them in each of the last 3 Octobers. A single Nashville Warbler seen Oct. 24 at New Providence was one 16 warbler species seen that day (BH), and Nashville and Orange-crowned warblers Oct. 28 were part of a 19 warbler day at Andros, BA (BH). Two Golden-winged Warblers were found at Guana Oct. 14 (FS, banded) & 18 (FS, unbanded). A Black-throated Blue Warbler seen Aug. 25 at Ferry Pt. Park, BE, provided the earliest record by 3 days. A Chestnut-sided Warbler, rarely seen in the Virgin Islands, was noted at a sugar feeder at Guana Oct. 18 (FS). A Bay-breasted Warbler was found at the South Ocean golf course, New Providence Oct. 26 (BH), one of the few times reported from the Bahamas.

Fourteen Bahama Yellowthroats were counted on a survey (TW, AB) from Treasure Cay to Sandy Pt., Abaco, Oct. 4. An important discovery was three Bahama Yellowthroats found Nov. 23 at Chub Cay, Berry Is., BA, where they were formerly considered hypothetical. A Summer Tanager was seen at Chub Cay Nov. 23. A Dickcissel was found in a flock of Bobolinks at New Providence Oct. 23 (PD) for one of the few records there.

A Chipping Sparrow, rarely found in the Bahamas, was noted at Grand Bahama Nov. 4 (TW). This was big season for Clay-colored Sparrows in the Bahamas. One was seen at North Andros Oct. 29 (JD); one in fields at Dover Sound, Grand Bahama, (BH); and one at Northwest Pt., Mayagauna, Oct. 25 (TW) for the first record there. A Grasshopper Sparrow at Pirate's Well, Mayaguana, Oct. 24 (TW, AB) provided a new record there (Buden 1987). A **White-throated Sparrow** was seen at West End Resort, Grand Bahama, Nov. 5 (BH) for a first record from the Bahamas.

A rare occurrence of Lapland Longspur at St. George's dairy, BE, Nov. 13 was the first since 1993. A Shiny Cowbird was found on Andros Oct. 28–29 in the company of Red-winged Blackbirds. Black-cowled Orioles seem to be hanging on nicely at Andros, where Hallett and Dunn found up to 12 on Oct. 28. A Com. Redpoll on Nov. 25 at St. David's, BE, was the first since November 1991.

ADDENDUM

Received too late to be included in the summer report are sightings from Bermuda. A White Ibis summered at Spittal Pond for the first time. A Gull-billed Tern at Nonsuch I. July 22 represented only the 2nd fall (late summer) report of the 12 ever recorded there. A very early Louisiana Waterthrush, 9 days ahead of a previous first fall date, appeared July 8, surpassing all other fall dates for any warbler species on Bermuda.

Contributors (sub-regional editors in boldface): Eric Amos, Audubon Naturalist Society, Ailene Bainton, Paul Dean, **Andrew Dobson**, Jon Dunn—WINGS, Daphne Gemmill, Bruce Hallett, Peter Holmes, Bruce Lorhan, Jeremy Madeiros, Carl Mowery, Henry Nixon, Roger Pocklington, Paul Reed, Fred Sibley, David Wallace, David Wingate, **Tony White**, Walker White.

Robert L. Norton, 3518 NW 37th Ave., Gainesville, FL 32605.

University of Wisconsin-Parkside
900 Wood Road, P.O. Box 2000
Kenosha, Wisconsin 53141-2000

College of Arts and Sciences
414/595-2327 Biological Science, Geology, Health Professions
414/595-2326 Chemistry, Mathematics, Physics
414/595-2056 FAX

phone:(414) 595-2074 email: mayerg@cs.uwp.edu fax:(414) 595-2056

4 May 1998

Dr. James D. Lazell, Jr.
The Conservation Agency
6 Swinburne St.
Jamestown, RI 02835

Dear Skip:

Enclosed are several copies of Rob Bleiweiss's paper that includes the Guana hummingbird data. He has at least a couple of more papers that use this hummingbird DNA hybridization data set to address other questions than the phylogenetic one addressed in this paper. One of these is already out (in PNAS, earlier this year), but I don't have reprints yet; I'll send you some when I do.

In the big paper (the one enclosed), Guana is explicitly cited, and he thanks you, Henry, Ralph, Rob Norton, Falconwood, and TCA. In the other papers, I think he refers to this one, and the species are mentioned, although Guana may not be explicitly mentioned (although it is by reference).

I have more copies if you need them for distribution.

Best wishes,

Gregory C. Mayer
Assistant Professor
Biological Sciences

DEPARTMENT OF ZOOLOGY

☐ ZOOLOGY RESEARCH BUILDING 1117 W. JOHNSON ST. ☒ BIRGE HALL 430 LINCOLN DR. ☐ LOWELL E. NOLAND HALL 250 N. MILLS ST.

UNIVERSITY OF WISCONSIN — MADISON

DEAR SKIP,

SORRY I COULDN'T ACKNOWLEDGE THE GUANA PROJECT DIRECTLY IN THE PAPER THAT "SPUN OFF" FROM THE MOLECULAR PHYLOGENY (ENCLOSED) - PAGE CHARGES & PAGE LIMITS ARE GETTING MORE RESTRICTIVE & REPEATING THE LENGTHY CITATION WAS PROHIBITIVE.

AS YOU WILL SEE, THE RESULTS W/ THE GUANA HUMMINGBIRDS WERE FASCINATING - WHO WOULD HAVE SUSPECTED THAT ORTHORHYNCUS WAS CLOSELY RELATED TO THE SABERWINGS (CAMPYLOPTERUS)! SOME INTERESTING IMPLICATIONS FOR BIOGEOGRAPHY TOO - BUT THESE AREN'T DUE OUT TILL LATER THIS YEAR IN BIOL. J. LINN. SOC. (2 LONG PAPERS).

WHERE WILL YOU HOLD THE SYMPOSIUM?

Best,
Rob

MADISON, WI 53706 TELEPHONE (608) 262-1051 FAX (608) 262-9083

DNA Hybridization Evidence for the Principal Lineages of Hummingbirds (Aves: Trochilidae)

Robert Bleiweiss, John A. W. Kirsch, and Juan Carlos Matheus†*

*Department of Zoology and the Zoological Museum, University of Wisconsin; and †Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador

The spectacular evolutionary radiation of hummingbirds (Trochilidae) has served as a model system for many biological studies. To begin to provide a historical context for these investigations, we generated a complete matrix of DNA hybridization distances among 26 hummingbirds and an outgroup swift (*Chaetura pelagica*) to determine the principal hummingbird lineages. FITCH topologies estimated from symmetrized ΔT_mH-C values and subjected to various validation methods (bootstrapping, weighted jackknifing, branch length significance) indicated a fundamental split between hermit (*Eutoxeres aquila, Threnetes ruckeri*; Phaethornithinae) and nonhermit (Trochilinae) hummingbirds, and provided strong support for six principal nonhermit clades with the following branching order: (1) a predominantly lowland group comprising caribs (*Eulampis holosericeus*) and relatives (*Androdon aequatorialis* and *Heliothryx barroti*) with violet-ears (*Colibri coruscans*) and relatives (*Doryfera ludovicae*); (2) an Andean-associated clade of highly polytypic taxa (*Eriocnemis, Heliodoxa,* and *Coeligena*); (3) a second endemic Andean clade (*Oreotrochilus chimborazo, Aglaiocercus coelestis,* and *Lesbia victoriae*) paired with thorntails (*Popelairia conversii*); (4) emeralds and relatives (*Chlorostilbon mellisugus, Amazilia tzacatl, Thalurania colombica, Orthorhyncus cristatus* and *Campylopterus villaviscensio*); (5) mountain-gems (*Lampornis clemenciae* and *Eugenes fulgens*); and (6) tiny bee-like forms (*Archilochus colubris, Myrtis fanny, Acestrura mulsant,* and *Philodice mitchellii*). Corresponding analyses on a matrix of unsymmetrized Δ values gave similar support for these relationships except that the branching order of the two Andean clades (2, 3 above) was unresolved. In general, subsidiary relationships were consistent and well supported by both matrices, sometimes revealing surprising associations between forms that differ dramatically in plumage and bill morphology. Our results also reveal some basic aspects of hummingbird ecologic and morphologic evolution. For example, most of the diverse endemic Andean assemblage apparently comprises two genetically divergent clades, whereas the majority of North American hummingbirds belong a single third clade. Genetic distances separating some morphologically distinct genera (*Oreotrochilus, Aglaiocercus, Lesbia; Myrtis, Acestrura, Philodice*) were no greater than among congeneric (*Coeligena*) species, indicating that, in hummingbirds, morphological divergence does not necessarily reflect level of genetic divergence.

Introduction

Hummingbirds (family Trochilidae) have undergone one of the most remarkable evolutionary radiations among birds. The allocation of more than 330 species into over 100 genera (Morony, Bock, and Farrand 1975) reflects a surprising morphological and physiological diversity modeled on the family's characteristic adaptations for nectar-feeding. Indeed, these varied attributes have enabled hummingbirds to occupy virtually every vegetated habitat in the New World, from humid tropical forest and arid deserts to the highest alpine zones (Bleiweiss 1991). Perhaps more than any other avian group of comparable extent, a considerable amount of information has been amassed about hummingbird diversity because of the relative ease with which their behaviors, ecologies, and energetic requirements can be quantified (Feinsinger and Colwell 1978).

Despite wide interest in the biology of hummingbirds, surprisingly little is known about the family's phylogeny. This gap in knowledge is due in part to the near absence of relevant fossils (Olson and Hilgartner 1982; Graves and Olson 1987) and to the difficulties of inferring relationships from the highly modified anatomy of these birds (Cohn 1968). Early hummingbird classifications drew attention to the fundamental distinction between so-called hermit and nonhermit hummingbirds, which were recognized as the subfamilies Phaethornithinae and Trochilinae, respectively (Gould 1861; Ridgway 1911). Although hermits and nonhermits originally were distinguished by superficial differences in plumage and trophic characters, several recent anatomical and molecular studies have supported monophyly of these two groups (Zusi and Bentz 1982; Gill and Gerwin 1989; Sibley and Ahlquist 1990; Bleiweiss 1991; Bleiweiss, Kirsch, and Matheus 1994). Other than this one feature of the family's phylogeny, however, broad relationships among hummingbirds remain poorly known. Indeed, hummingbird classifications still are based largely on 19th century studies, and with few exceptions (Zusi and Bentz 1982; Sibley and Ahlquist 1990; Bleiweiss, Kirsch, and Lapointe 1994; Bleiweiss, Kirsch, and Matheus 1994), modern systematic treatments have focused mostly on species-level questions or on circumscribed genera (Stiles 1983; Bleiweiss 1985, 1988*a*, 1988*b*, 1992*a*, 1992*b*; Graves 1986; Schuchmann 1987; Gerwin and Zink 1989; Gill and Gerwin 1989; Escalante-Pliego and Peterson 1992).

Our earlier DNA hybridization study comparing eight tropical hummingbirds (Bleiweiss, Kirsch, and Matheus 1994) addressed the question of monophyly for the two traditional subfamilies. Here we apply the same technique to a much broader set of comparisons with the aim of identifying the principal lineages among the

Key words: DNA hybridization, phylogeny, hummingbirds, hermit, nonhermit, Andes.

Address for correspondence and reprints: Robert Bleiweiss, Department of Zoology and the Zoological Museum, University of Wisconsin, Madison, Wisconsin 53706. E-mail: reb@ravel.zoology.wisc.edu.

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diverse nonhermits. This putative group of over 300 recognized species contains the bulk of the family's taxonomic and morphologic diversity and is much more widespread geographically than the largely tropical hermits (Bleiweiss 1991). One of our objectives was to reexamine the deepest structure of the phylogeny, because our limited earlier comparisons did not rule out the possibility that some lineage or lineages diverged prior to the split between hermits and their sister group. In particular, Ridgway (1911) recognized a third subfamily, Lophornithinae, composed of highly ornamented diminutive forms, the so-called coquettes, which we had not examined. More generally, we sought to expand coverage of ecological diversity by including representatives from throughout the family's geographic range. Finally, the broader sampling of taxa would presumably illuminate the complicated taxonomy of hummingbird genera, of which over half are monotypic (Morony, Bock, and Farrand 1975). Many of these taxa are based on distinctive plumage features that are suspect indicators of either level of genetic divergence or cladistic relationship (Banks and Johnson 1961; Mayr and Short 1970).

To provide this broad overview, we were motivated to undertake the largest complete matrix ever attempted with DNA hybridization. Our study confirms that the deepest split among hummingbirds distinguishes hermits and nonhermits, provides strong support for six principal and many subsidiary clades of nonhermits, and thus provides the first well-supported molecular phylogenetic framework for the family.

Materials and Methods

Selection of Taxa

The taxonomic scope of any DNA hybridization study is limited in practice, because cladistic relationships can be reliably distinguished from rate variation only by a complete set of reciprocal distances, whose number increases with the square of the number of taxa (Barrowclough 1992; Lapointe and Kirsch 1995). The taxa we chose to compare encompassed major groups suggested by several earlier studies: (1) the standard linear arrangement for hummingbirds (exemplified by Peters 1945; Monroe and Sibley 1993), which incorporates the results of many early studies of hummingbird systematics (Gould 1861; Elliot 1879; Boucard 1895; Hartert 1900; Ridgway 1911; Simon 1921); (2) the recent anatomical work of Zusi and Bentz (1982) that distinguished four groups of hummingbirds based on differences in the wing muscle tensor propatagialis pars brevis (TPB); (3) the more limited DNA hybridization studies of Sibley and Ahlquist (1990) and Bleiweiss, Kirsch, and Matheus (1994), which provide the only other published molecular studies of higher-level relationships among nonhermits. Together, our comparisons include approximately 25% of recognized genera, which themselves subsume almost 45% of known species (table 1).

Given the absence of any other detailed guide to broad relationships among hummingbirds, the standard linear sequence provides the only available introduction to the species in our study (table 1). In addition to two hermits (*Eutoxeres aquila* and *Threnetes ruckeri*), we selected several taxa that immediately follow hermits and which are considered primitive among nonhermits, including two whose dull-colored plumages resemble those of hermits (*Androdon aequatorialis* and *Doryfera ludovicae*) as well as four iridescent forms (*Eulampis holosericeus, Colibri coruscans, Orthorhyncus cristatus* and *Campylopterus villaviscencio*). Of the three genera Ridgway (1911) included in his Lophornithinae, we obtained sufficient tissues from the thorntail *Popelairia conversii*. From the host of emeralds and their presumed relatives, we selected typical green-colored forms (*Amazilia tzacatl* and *Chlorostilbon mellisugus*) and the distinctive woodnymphs (*Thalurania colombica*) listed near them. We included two sorts of taxa from the exceptionally rich Andean communities: representatives from some of the most polytypic genera (*Oreotrochilus chimborazo, Eriocnemis luciani, Heliodoxa jacula*, and *Coeligena* spp.) and from distinctive long-tailed genera (*Aglaiocercus coelestis* and *Lesbia victoriae*) of uncertain relationship. We also included both large-bodied taxa that breed north of Mexico (*Lampornis clemenciae* and *Eugenes fulgens*). Among taxa listed near the end of the standard sequence, we included *Heliothryx barroti*, because it shares the type II condition of TPB with some of the presumed primitive taxa, as well as four genera from among the tiny bee-like forms that conclude the sequence. The bees we compared encompassed forms with both the taxonomically widespread type III and the more restricted type IV condition of TPB (table 1), and ones found in North (*Archilochus colubris*), Central (*Philodice mitchellii*) and South (*Myrtis fanny* and *Acestrura mulsant*) America.

Based on evidence for their sister relationship to nonhermits, hermits provide one potential outgroup for rooting the nonhermit tree (Sibley and Ahlquist 1990; Bleiweiss, Kirsch, and Lapointe, 1994; Bleiweiss, Kirsch, and Matheus 1994). However, as stated above, the limited nature of these earlier comparisons allows for the possibility that some currently recognized nonhermits are actually basal to the hermits (e.g., the possible subfamily status of Ridgway's Lophornithinae). Broader studies comparing additional nonhumingbird taxa have identified swifts as the sister group to hummingbirds, the two clades comprising the monophyletic Apodiformes (Sibley and Ahlquist 1990; Bleiweiss, Kirsch, and Lapointe 1994). Hence, swifts provide an unambiguous outgroup for rooting any hummingbird phylogeny. Inclusion of both hermits and swifts has the additional advantage that simulation studies indicate that multiple outgroups improve accurate placement of the root, especially if several representatives of the nearest outgroup are included (Smith 1994). Thus, we included representatives from the two most divergent hermit genera (*Eutoxeres aquila* and *Threnetes ruckeri*) and the typical swift *Chaetura pelagica* (family Apodidae). Unfortunately, swifts and hummingbirds are themselves distant relatives (Sibley and Ahlquist 1990; Bleiweiss, Kirsch, and Lapointe 1994) such that no other taxa exist to subdivide the long branch between them; additional

Table 1
Taxa Examined

Latin Name	Common Name	Number of Congeners	TPB
Threnetes ruckeri	Band-tailed barbthroat	3	I
Eutoxeres aquila	White-tipped sicklebill	2	I
Androdon aequatorialis	Tooth-billed hummingbird	1	II
Doryfera ludovicae	Green-fronted lancebill	2	II
Campylopterus villaviscensio	Napo saberwing	11	III
Colibri coruscans	Sparkling violet-ear	4	II
Eulampis holosericeus[a]	Green-throated carib	2	II
Orthorhyncus cristatus	Antillean crested hummingbird	1	III
Popelairia conversii[b]	Green thorntail	4	III
Chlorostilbon mellisugus	Blue-tailed emerald	13	III
Thalurania colombica	Blue-crowned woodnymph	6	III
Amazilia tzacatl	Rufous-tailed hummingbird	30	III
Lampornis clemenciae	Blue-throated hummingbird	6	III
Heliodoxa jacula[c]	Green-crowned brilliant	9	III
Eugenes fulgens	Magnificent hummingbird	1	III
Oreotrochilus chimborazo[d]	Ecuadorian hillstar	5	III
Coeligena wilsoni	Brown Inca	10[e]	III
Coeligena torquata	Collared Inca	10	III
Eriocnemis luciani	Sapphire-vented puffleg	10	III
Lesbia victoriae	Black-tailed trainbearer	2	III
Aglaiocercus coelestis	Violet-tailed sylph	2	III
Heliothryx barroti	Purple-crowned fairy	2	II
Philodice mitchellii	Purple-throated woodstar	2	III
Archilochus colubris	Ruby-throated hummingbird	2	III
Myrtis fanny	Purple-collared woodstar	1	III
Acestrura mulsant	White-bellied woodstar	5	IV
Chaetura pelagica	Chimney swift	?	NA[f]

GUANA

NOTE.—Taxa are listed by their order in the taxonomic list of Monroe and Sibley (1993). Number of congeners and condition of tensor propatagialis pars brevis (TPB) described by Zusi and Bentz (1982) also indicated.

[a] Sometimes placed in the monotypic genus *Sericotes* (American Ornithologists' Union 1983).

[b] Sometimes placed in the genus *Discosura* (American Ornithologists' Union 1983).

[c] Includes previously recognized monotypic genus *Polyplancta* (Gerwin and Zink 1989).

[d] Sometimes considered a subspecies of *Oreotrochilus estella*.

[e] *Coeligena orina* doubtfully a distinct species within genus (Bleiweiss 1988*a*).

[f] Not applicable

swifts would only subdivide the long intervening branch near the tip. Thus, some limits on outgroup design are imposed by which apodiform lineages have survived.

Sample Preparation

All tissue samples were collected by Bleiweiss with collaborators on field trips to Wisconsin and Arizona in the United States, the British Virgin Islands in the Caribbean, and Ecuador on the South American mainland (appendix 1; see *Acknowledgments*). Methods for field preservation and laboratory extraction of DNA followed those outlined in Bleiweiss, Kirsch, and Matheus (1994) with the following modifications. Single-copy tracers were prepared by boiling and then incubating 400 μg of DNA at 60°C in 0.48 phosphate buffer to C_0t 400 (Equivalent C_0t 2260), after which the sample was diluted to 0.12 M and subsequently eluted over 1.0-ml hydroxyapatite (HAP). Hybrids were fabricated in 1.0 ml snap-cap vials by adding 0.05 μg of ^{125}I-labeled tracer DNA to 25 μg of driver DNA diluted in 0.48 M phosphate buffer to a standard concentration (3.0 μg/μl) and volume (8.3 μl). All 75 hybrids for a given label were placed in three sets of floating plastic boats and boiled simultaneously for 8 min. Hybrids were immediately incubated at 60°C to an EC_0t of approximately 24,000 and then quick-frozen. Prior to loading, each hybrid was diluted to 0.12 M phosphate buffer by adding 325 μl of 0.11 M phosphate buffer, mixed briefly with a vortexer, and pipetted onto a column of 0.5 ml of HAP. Fractionation began with two room-temperature washes to remove unhybridizable DNA and free iodine, followed by 23 fractionations obtained by pumping 0.12 M phosphate buffer over 0.5 ml HAP at 2°C increments starting with 8 ml at 52°C and changing to 5 ml for all succeeding washes up to 96°C. Elution fractions were counted within 24 h of collection.

Experimental Design

Generation of unbiased genetic distance estimates requires careful attention to experimental design (Bleiweiss and Kirsch 1993*a*, 1993*b*). Several precautions were taken to limit systematic biases, as detailed in Bleiweiss, Kirsch, and Matheus (1994). In addition, we tailored our experiments to obtain unbiased measures of the median melting temperature (T_m). This index is emphasized here because it incorporates information about more sequences (because it is calculated over practically the entire range of elution temperatures) and is better characterized at that level than alternative indices (Sheldon and Bledsoe 1989; Springer, Davidson, and Britten 1992; Bleiweiss and Kirsch 1993*b*). As a more inclusive measure of divergence than other indices (e.g., T_{mode}), it

is unsurprising that previous experiments have demonstrated T_m's sensitivity to individual genetic differences (Bleiweiss and Kirsch 1993*b*). To obtain the best variance estimates, therefore, each replicate comparison was made with DNA extracted from a different individual. A drawback to this design is that homologous (same species) duplexes that serve as standards for calculating genetic distances melt at slightly lower temperatures *on average* when the two strands come from a different (allologous) rather than the same (autologous) individual (unpublished data); consequently, branch lengths measured from allologous homologues will be shortened very slightly. Elsewhere, we show that topological relations remain unchanged by inclusion or exclusion of the allologous homologues (unpublished data). The effect on branch lengths can be mitigated to a certain extent through application of corrections for variation in the melting temperature among homologous hybrids, as detailed below. We used allologous homologues so as to obtain better estimates of random variation in homologous melting temperatures, which otherwise would be underestimated by use of multiple preparations from the single extract (Bleiweiss and Kirsch 1993b) that can be made in practice from most hummingbirds. Intraspecific hybrid DNAs are useful also because they provide a conservative measure of imprecision in homologous melting temperatures and also serve as an internal control for interspecific comparisons. Therefore, we used one autologous and two allologous homologues for each taxon. We also included congeneric species (two of *Coeligena*) to provide some measure of intrageneric divergence for the evaluation of higher-level taxonomy.

As our thermal elution device (TED) for fractionating DNA-DNA hybrids (Kirsch et al. 1990) holds only 25 columns, we employed the following design to generate the complete matrix of reciprocal comparisons among 27 taxa. For each labeled taxon, a standard set of 20 species was represented by a different individual on each of three TED runs. Another set of six taxa (*Chaetura pelagica, Threnetes ruckeri, Heliothryx barroti, Heliodoxa, Coeligena torquata,* and *Campylopterus villaviscencio*) was represented by different individuals on the first two of these runs and then replaced by three individuals each of an additional two taxa (*Myrtis fanny* and *Philodice mitchellii*) on the third run. The complete 27 × 27 matrix with corresponding numbers of replicates per comparison (3 for 22 species, and 2 for 6 species) required 81 runs of the TED.

Indices and Data Transformations

We transformed T_m in several steps to obtain the most accurate estimates of genetic distance. To compensate for underestimates of genetic divergence due to hybridizable DNA that failed to form stable hybrids at criterion temperature (percentage of hybridization), we corrected T_m for the normalized percentage of hybridization (NPH), which is defined as:

$$\text{NPH} = \frac{(\text{percentage of hybridization})\text{heterologue}}{(\text{percentage of hybridization})\text{homologue}},$$

where percentage of hybridization is calculated as the number of counts eluted at and above criterion temperature (56°C in 0.12 M phosphate buffer) over the total number counts (52–96°C under the same conditions). The corrected index, T_{50}H, was then obtained by normalizing the heteroduplex curve with NPH, as described in Werman, Springer, and Britten (1996). To avoid the large experimental errors typically associated with NPH (Bleiweiss and Kirsch 1993*a*, 1993*b*), we used the functional relationship between the observed values of T_m and T_{50}H to generate expected values of T_{50}H from their associated T_m's. Backward elimination of nonsignificant higher-order terms indicated that, for our data, this relationship was best described by a second-order polynomial:

$$T_{50}\text{H} = 4.50T_m - 0.0212(T_m)^2 - 145.$$

The expected T_{50}H values were then corrected for multiple mutations at single base sites by first converting melting temperatures to measures of percent sequence divergence (Springer, Davidson, and Britten 1992), and then correcting them for homoplasy with the equation of Jukes and Cantor (1969). Typically, these transformations are applied to the final matrix of mean Δ values, which measures the average distance of individual heterologues from the average homologous melting temperature for that label. However, to retain replicate values so that they could be subjected to the randomization and validation tests described below, we deviated from this usual practice and applied corrections to the melting temperature of each hybrid. The mathematical properties of the Jukes-Cantor correction required that each raw melting value first be converted to a Δ value. To accomplish this, we used the single autologous hybrid as the standard because it is the most accurate measure of the homologous melting temperature. Following transformation, these Δ values were converted back to the original scale by subtracting them from the untransformed autologous T_{50}H values (which remained untransformed for the reasons stated above). Thus, the final fully corrected values of T_mH-C were obtained by the following equation:

$$T_m\text{H-C} = \text{HOM} - (-0.75\ \ln(1 - 4/3((\text{HOM} - \text{HET}) \times 1.2)/100)100),$$

where HOM is the raw T_{50}H melting temperature of the autologous standard for that taxon, HET is the same for the heterologue, and 1.2 is the empirically determined slope of the relationship between ΔT_m and percent sequence divergence (Springer, Davidson, and Britten 1992).

Prior to these calculations, we excluded individual hybrids with anomalously low NPHs (<75% for hummingbirds, <55% for swift) that we determined were due to water leaking into the incubating hybrid (see also Sheldon and Winkler 1993). Even so, such cases amounted to only 23 hybrids, or approximately 1% of the 2,025 experimental hybrids run in the TED. The final matrix of Δ values was subjected to A. W. Dickerman's program SYMMETRY, which corrects for compression of Δ values often associated with lower-melting homologous hybrids by the method of Sarich and Cronin

(1976; see also Springer and Krajewski 1989; Springer and Kirsch 1989, 1991). The theoretical justification for this procedure is that it improves the metrical properties of the distance matrix by correcting for asymmetries in reciprocal comparisons which otherwise violate the assumptions of distance methods of tree reconstruction. At the same time, symmetrization eliminates a ubiquitous source of systematic experimental error that could be confounded with rate variation. We also analyzed unsymmetrized matrices, and ones in which the percent sequence divergence and homoplasy corrections were applied to the matrix of averaged Δ values rather than to the individual replicates, thereby allowing us to examine possible effects of the various transformations and the order of their application on the resulting topologies.

Data Analysis

Our complete matrices of unsymmetrized and symmetrized Δ values permit use of the FITCH routine in Felsenstein's PHYLIP (version 3.5c, 1993) to obtain topologies by least-squares criteria without the assumption of rate uniformity, as mandated in the alternative KITSCH routine. The correlation between the standard deviations of replicate measures and distance was nonsignificant ($r = 0.177$, df = 25, $P \gg 0.10$) for the 26 hummingbirds but increased to marginal nonsignificance ($r = 0.425$, df = 25, $P < 0.10$) with inclusion of the swift (see appendix 2). Despite the apparent greater variability of replicate measures in the distant outgroup swift suggested by this difference, we adopted the Cavalli-Sforza and Edwards (1967) unweighted least-squares method (zero exponent in the denominator of the equation for calculating sum-of-squares) as the most appropriate method for assessment of hummingbird relationships, which was our primary focus. Use of this method also is more conservative in that it necessarily increases the unexplained sum-of-squares by reducing the value of the denominator (to one).

A number of validation methods were applied to examine the robustness of the topologies. To test the null hypothesis that matrices lacked structure, we used a modified Mantel test to determine the significance of z scores,

$$z = \text{mean } SS_{\text{randomized matrices}} - SS_{\text{observed matrix}}/SD_{\text{randomized matrices}} SS$$

from the mean sum-of-squares (SS) and their standard deviation (SD) of a distance matrix whose columns had been randomized 100 times while holding the zero diagonals fixed.

We applied Krajewski and Dickerman's (1990) bootstrap method for distance data to determine the effects of within-cell variation in replicate measures on topologic consistency. One thousand pseudoreplicate matrices were generated with A. W. Dickerman's program, BOOTTEMP, which samples with replacement each cell in the original matrix. The resulting pseudoreplicate matrices were each subjected in turn to FITCH with subreplicate and global branch-swapping options enabled, negative branch lengths disallowed, and the input order of taxa randomized (using the jumble option). The CONSENSE program in PHYLIP was then used to obtain the consensus among the 1,000 trees, and thus to determine the level of support for each node. We then calculated average pathlengths among each set of 1,000 best-fit topologies using the programs TRANSLATOR and NONSENSUS (written by F. J. Lapointe). To determine if branch lengths differed significantly from zero, we first calculated the standard deviation of each branch over the 1,000 trees generated from random pseudomatrices, each constrained by the topology obtained for the corresponding data treatment. We then applied the standardized normal deviate (z) test of Rzhetsky and Nei (1992, 1993), using the critical value for $P < 0.05$ as the criterion for rejection of the null hypothesis of zero length.

Finally, the stability of topological relationships to changes in the taxonomic composition of the matrix was tested by the average-consensus procedure for weighted jackknife trees (Lapointe, Kirsch, and Bleiweiss 1994). This algorithm weights the stability of a node by its associated pathlength between the two terminal taxa joined by it, thereby incorporating more information from the distance matrix than do strict-consensus methods (Lanyon 1985). The program for performing weighted jackknifes (JACKMAT; written by F. J. Lapointe) also allows for more exhaustive explorations of the robustness of jackknifed trees through options for specified or random multiple deletions of taxa. In our case, it was impractical to sample an appreciable fraction of the more than 134×10^6 possible combinations of 4 to 26 taxa by the random (or exhaustive) deletion method. Previous studies have observed (Lapointe, Kirsch, and Bleiweiss 1994) that sequential deletions of $n + 1$ taxa eventually produce a stable topology (and one which matches a "global" or all-possible-deletions test), implying that further deletions have no effect, and this strategy was adopted.

Table 2
Summary Statistics on Tablewide Average Within-Cell Standard Deviation (SD) and Percent Nonreciprocity (Asymmetry) for Values in Appendix 2

	Observed ΔT_m	Observed ΔNPH	Observed $\Delta T_{sq}H$	Estimated $\Delta T_{sq}H$-C
Mean SD.....	0.200	1.723	0.335	0.338[a]
Asymmetry[b] ...	3.86/1.86	27.18/27.55	4.79/2.40	4.28/2.14

[a] Increased scaling of $\Delta T_{sq}H$-C increases mean SD relative to that of measured $\Delta T_{sq}H$.
[b] Initial asymmetry/final asymmetry.

Results

Data Characteristics

The data provide an exceptionally large number of comparisons on which to base inferences about hummingbird relationships (appendix 2). The variability of replicate measures of T_m and NPH clearly demonstrate the much higher error associated with the latter index alone or when combined with T_m into the composite $T_{sq}H$ index (table 2). The tablewide average within-cell

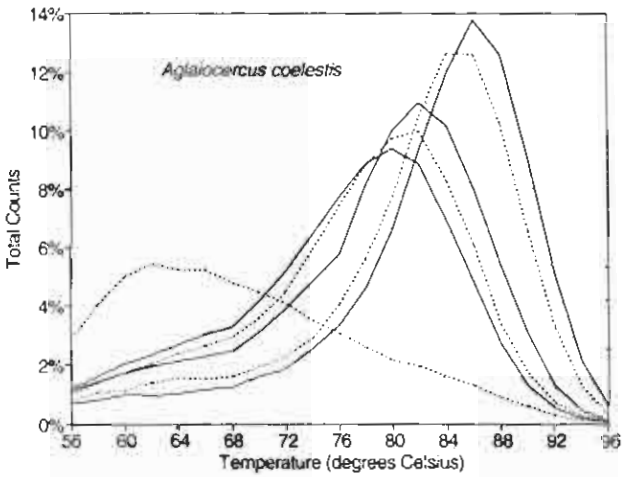

FIG. 1.—Representative thermal-elution curves for labeled violet-tailed sylph (*Aglaiocercus coelestis*). From right to left, curves are for *Aglaiocercus coelestis* (homologue), *Lesbia victoriae*, *Popelairia conversii*, *Androdon aequatorialis*, *Threnetes ruckeri*, and *Chaetura pelagica*.

standard deviations for T_m and for $T_{50}H$ (table 2) apparently are lower than those reported in most previous DNA hybridization studies (see Krajewski 1989; Bleiweiss and Kirsch 1993*b*; Sheldon and Winkler 1993; Bleiweiss, Kirsch, and Matheus 1994), however, indicating that our data are unusually precise even though each within-cell replicate was generated with DNA from a different individual. Thus, conversion of T_m to $T_{50}H$ by the regression procedure also should provide relatively more precise measures of $T_{50}H$ and the fully corrected T_mH-C. Representative stepwise melting curves made with labeled *Aglaiocercus coelestis* demonstrate overall high levels of discrimination among the many hummingbird taxa (fig. 1), despite ΔT_mH-C values which are all within 0.5–12°C (appendix 2). The high NPH among hummingbird hybrids (>85%) contrasts with much lower values for swift-hummingbird hybrids (60%–70%; see also the reduced area subtended by its elution curve in fig. 1, where the individual elutions have been corrected for percentage of hybridization of the relevant hybrid), reaffirming the distant relationship between hummingbirds and the latter.

Matrix Characteristics

In addition to imprecision in replicate values, inaccuracies of various sorts could distort the distance matrices and topologies estimated from them. For example, applying corrections for percent sequence divergence and homoplasy directly to the replicates might produce results that differ from those obtained when these corrections are applied to average cell values of the matrices themselves. In the present case the two treatments appear to produce exceptionally similar relationships among Δ values, as distance matrices based on the different procedures are very highly correlated (table 3). More directly, even the fitted pathlength matrices for FITCH topologies constructed from corresponding distance matrices are highly correlated with each other (table 3). Thus, the data appear very robust to the order in which corrections were applied. The marginally lower correlations between corresponding distance and pathlength matrices nonetheless indicate that the measured distances adhere very closely to the least-squares assumption of additivity inherent in the pathlength matrices. The somewhat higher correlations between distance and pathlength matrices that are symmetrized (table 3) suggest that the matrix asymmetry corrections (of about 2%; appendix 2, table 3) improve additivity somewhat.

Table 3
Pearson Correlations for Distance (D) and Pathlength (P) Matrices in Which Percent Sequence-Divergence and Jukes-Cantor Corrections Were Made on Replicate Δ Values (r) or on the Matrix (m)

	D_m	D_r	P_m	P_r
D_m	—	**0.99987**	**0.99639**	**0.99635**
D_r	0.99998	—	**0.99721**	**0.99719**
P_m	0.99637	0.99632	—	**1.00000**
P_r	0.99636	0.99632	1.00000	—

NOTE.—Values for symmetrized matrices are indicated in boldface. Tests were conducted using the matrix comparison progcam (MXCOMP) in NTSYS-pc (Rohlf 1992). All correlations are highly significant ($P < 0.0001$) by Mantel test on z scores.

The presence of a single long branch to a distant outgroup as in our set of comparisons (the swift *Chaetura pelagica*) may bias a Mantel test toward rejection of the null hypothesis of no matrix structure by contributing disproportionately to the value of the z score. To provide a more conservative test, we therefore eliminated the swift prior to randomization of the matrix. Even with this modification, very significant structure is indicated for both unsymmetrized ($z = 34.31$, $P < 0.0001$) and symmetrized ($z = 42.35$, $P < 0.0001$) matrices. Unsurprisingly, symmetrization increases the value of the z score, as this correction reduces random distortions in the matrix due to variation in homologous melting temperatures.

Phylogeny

FITCH topologies obtained by first correcting the data for percent sequence divergence and homoplasy prior to matrix construction (figs. 2 and 3) are identical to those obtained by correcting the matrix (unpublished data; also found in a previous study by Kirsch, Dickerman, and Reig 1995). The results based on corrected replicates are discussed here because they allow for application of bootstrap resampling tests. Both unsymmetrized and symmetrized topologies appear to provide exceptionally robust estimates of hummingbird phylogeny and agree on many basic aspects of hummingbird relationships (figs. 2 and 3). In general, support was low only for a few very short internodes in the tree (figs. 2 and 3). Validation tests provide strong support for the majority of branches in both topologies (figs. 2, 3). Only two internodes, both in the unsymmetrized tree, were sensitive to jackknifing (indicated by dotted lines); for both unsymmetrized and symmetrized matrices, the results of performing all 2,925 possible combinations for three deleted taxa were identical to those of performing all 351 combinations for two deleted taxa, and no further

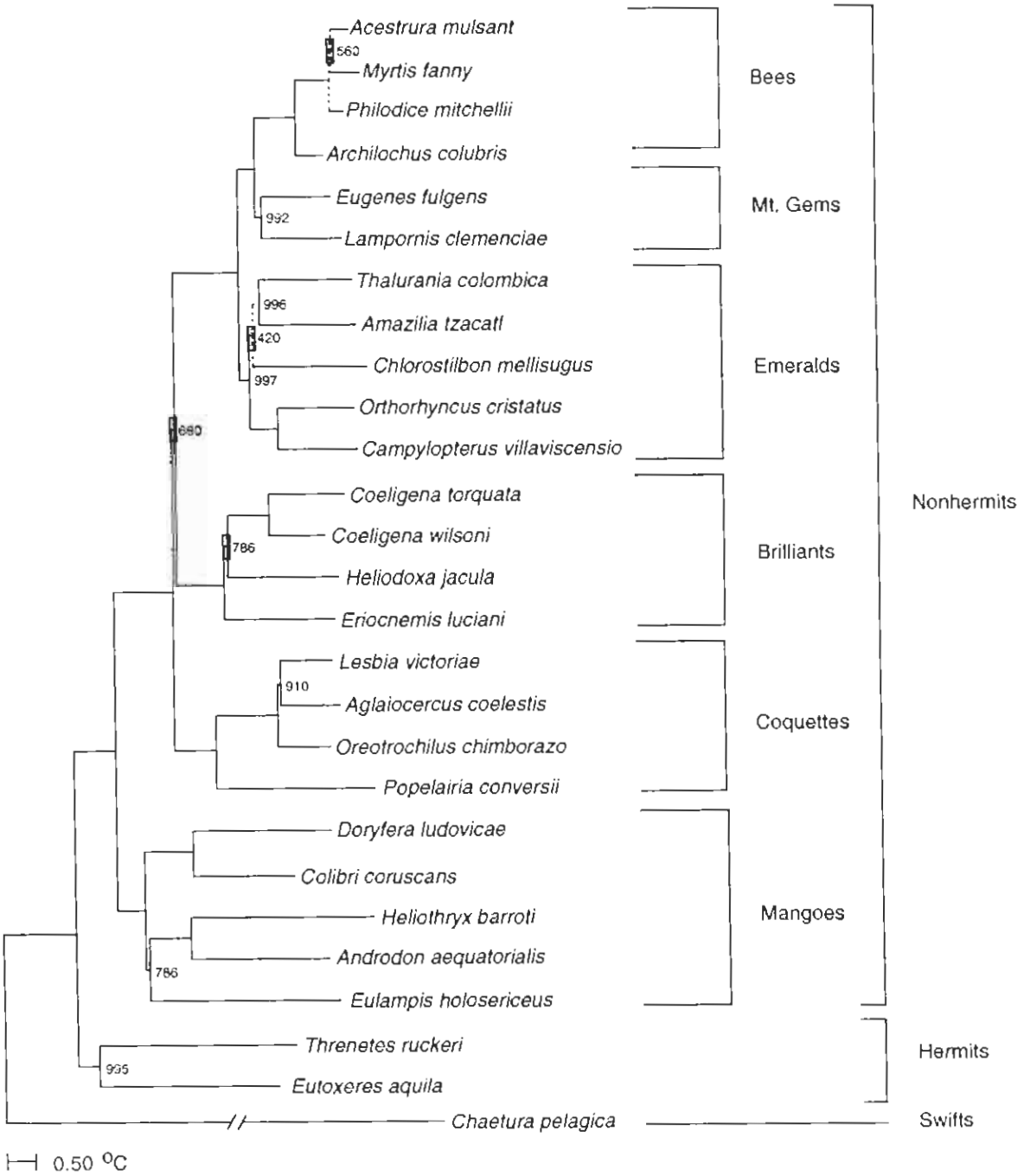

FIG. 2.—Consensus bootstrap FITCH topology based on unsymmetrized ΔT_{50}H-C. Branch lengths are averages over the 1,000 bootstrap pseudoreplicate trees and for hummingbirds are drawn to scale. Dashed lines indicate nodes that collapse in jackknifing, percentages indicate support out of 1,000 bootstrap pseudoreplicate trees (if less than 100%), and gray bars indicate nodes that are not significantly different from zero length. Clade names are as described in text.

deletion sets were examined. Similarly, no more than three internodes per tree received low bootstrap support (defined here as less than 700 out of 1,000 pseudoreplicates), and in the unsymmetrized tree these were the same internodes that collapsed under jackknifing. Internodes that were not supported by jackknifing and/or which received low bootstrap support typically were those whose branch lengths were not significantly different from zero (gray bars).

In all analyses, the swift rooted hummingbirds between the 2 traditional hermit genera (*Eutoxeres aquila* and *Threnetes ruckeri*) and the remaining 24 nonhermits. No taxon ever joined the tree outside this fundamental split. Thus, even among the taxa in our expanded comparisons, the traditional hermits and nonhermits remain sister groups that define the deepest bifurcation among extant members of the family. This outcome indicates that the 2 hermits do comprise a near outgroup

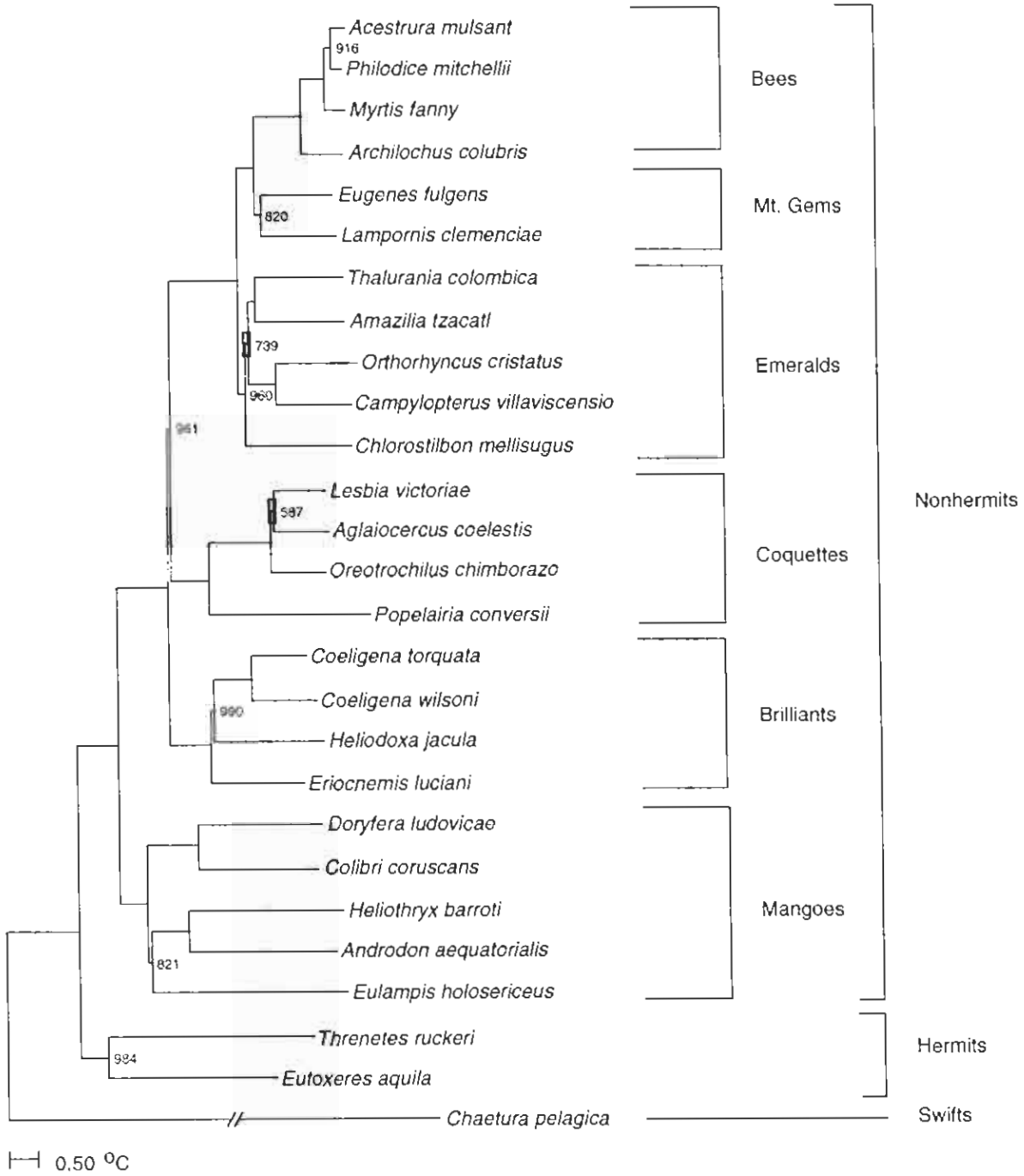

FIG. 3.—Consensus bootstrap FITCH topology based on symmetrized ΔT_mH-C. Branch lengths are averages over the 1,000 bootstrap pseudoreplicate trees and for hummingbirds are drawn to scale. Dashed lines indicate nodes that collapse in jackknifing, percentages indicate support out of 1,000 bootstrap pseudoreplicate trees (if less than 100%), and gray bars indicate nodes that are not significantly different from zero length. Clade names are as described in text.

for rooting the remaining 24 nonhermits, which allows for further testing of ingroup relations when only hermits are used to root the tree. Topologies obtained in this way (i.e., eliminating the swift) are otherwise identical to those for the full suite of 27 taxa (unpublished data).

Within the nonhermits, six principal groups were supported strongly by all analyses. To facilitate discussion, we name each of them after a characteristic member: (1) **mangoes**: a varied assemblage of many lowland forms that includes caribs (*Eulampis holosericeus*), fairies (*Heliothryx barroti*), violet-ears (*Colibri coruscans*), the hermit-like lancebills (*Doryfera ludovicae*) and the tooth-billed hummingbird (*Androdon aequatorialis*); (2) **brilliants**: an Andean clade of highly polytypic genera including brilliants (*Heliodoxa jacula*), incas (*Coeligena wilsoni* and *C. torquata*), and pufflegs (*Eriocnemis luciani*); (3) **coquettes**: a second clade of endemic high-

Andean genera including hillstars (*Oreotrochilus chimborazo*), sylphs (*Aglaiocercus coelestis*) and trainbearers (*Lesbia victoriae*) paired with the lower-elevation thorntails (*Popelairia conversii*); (4) **emeralds**: various genera including typical green-colored (*Chlorostilbon mellisugus* and *Amazilia tzacatl*) and other (*Thalurania colombica, Orthorhyncus cristatus*, and *Campylopterus villaviscensio*) forms; (5) **mountain-gems:** the large-bodied *Lampornis clemenciae* and *Eugenes fulgens*; and (6) **bees**: tiny forms comprising several genera (*Archilochus colubris, Myrtis fanny, Philodice mitchellii*, and *Acestrura mulsant*). Three basic features of cladistic structure are strongly supported in all analyses: the basal position of the clade that includes mangoes, violet-ears, and their relatives; a sister relationship between bees and mountain-gems; and a sister relationship between these two and the emerald assemblage. Unsymmetrized and symmetrized data differ in their placement of the two principal Andean clades (2 and 3 above), which depends on alternate arrangements around a short internode. For unsymmetrized data, the internode is 0.0198°C and places coquettes and their allies (3 above) outside the sister-pairing of the second Andean clade plus the emeralds–mountain-gems–bee lineage (fig. 2). However, this arrangement fails the branch length test of nonzero length, and receives only moderate bootstrap support (68%). For symmetrized data, by contrast, the pivotal internode is 0.0728°C and all three validation tests provide strong support for placement of the polytypic Andean clade (2 above) outside the other principal Andean lineage (fig. 3).

Our data also provide strong support for most associations within these principal nonhermit lineages. All analyses and validation methods support two lineages within the mango clade, one defined by *Colibri coruscans–Doryfera ludovicae* and the other including *Eulampis holosericeus* and the sister pair of *Androdon aequatorialis–Heliothryx barroti*. All analyses indicate 100% support for a sister-group relationship between the thorntail *Popelairia conversii* and the trio of endemic and highly distinctive Andean taxa *Oreotrochilus chimborazo, Aglaiocercus coelestis*, and *Lesbia victoriae*. Although the two long-tailed forms *Aglaiocercus coelestis* and *Lesbia victoriae* are paired in both unsymmetrized and symmetrized trees, the arrangement for symmetrized data fails the branch-length test and receives low bootstrap support. In the second clade of largely Andean forms, both *Coeligena* species are always paired, and associate with *Heliodoxa jacula* to the exclusion of *Eriocnemis luciani*. However, for unsymmetrized data, the position of *Eriocnemis luciani* as the first branch in this clade fails the branch-length test.

Among the emeralds and their allies, the trees strongly support sister relationships between *Orthorhyncus cristatus* and *Campylopterus villaviscencio* and between *Thalurania colombica* and *Amazilia tzacatl*. The interrelationship between these two groups depends on the more problematic placement of *Chlorostilbon mellisugus*, which defines the sister group to *Thalurania colombica–Amazilia tzacatl* for unsymmetrized data, but the sister group to the entire assemblage for symmetrized data. However, the former arrangement receives low bootstrap support and collapses under jackknifing and branch-length tests, whereas the latter placement fails the branch-length test. The sister-group relationship of mountain-gems and bees is always strongly supported, as is the sister relationship of *Archilochus colubris* to the remaining, more southern, forms of bees. Among the latter, *Acestrura mulsant* pairs with *Myrtis fanny* for unsymmetrized data but with *Philodice mitchellii* for symmetrized data. Only the arrangement for symmetrized data receives strong support from all three validation tests.

Discussion

DNA hybridization has been subjected to intense scrutiny both as to what it measures and how best to analyze the data (Cracraft 1987; Houde 1987; Marks, Schmid, and Sarich 1988; Sarich, Schmid, and Marks 1989; Springer and Krajewski 1989; O'Hara 1991; Raikow 1991; Lanyon 1992). While such aspects of DNA hybridization have been examined in the literature, in part by ourselves (Bleiweiss and Kirsch 1993*a*, 1993*b*; Lapointe, Kirsch, and Bleiweiss 1994; Bleiweiss, Kirsch, and Shafi 1995; Lapointe and Kirsch 1995), the novel feature of the present study is one of scale. Both the size of our complete matrix and that of the group analyzed are substantially larger than those usually tackled with DNA hybridization. Thus, we focus on technical issues that likely relate to matrix size, including taxonomic sampling bias, level of replication, and topologic stability.

The issue of taxonomic sampling bias is important for DNA hybridization studies of large evolutionary radiations because of the method's practical limitations on the number of taxa for which one can obtain a full suite of reciprocal comparisons. Although our complete matrix is the largest ever generated, our comparisons represent only a fraction of hummingbird diversity, possibly creating taxonomic sampling biases that affect topology construction (Smith 1994; Swofford et al. 1996). Such biases are difficult to detect in practice because they can nevertheless produce topologies that receive strong support from validation methods (Philippe and Douzery 1994; Adachi and Hasegawa 1996). We believe that our phylogeny will prove robust to additional comparisons because it appears to avoid many known sources of such inaccuracies. For example, sparse sampling in which genetically distinct clades are represented by one taxon may produce topological artifacts due to the propensity of the divergent singletons to associate because of homoplastic similarities resulting from saturation of base substitutions. This is unlikely to be a problem for our matrix for several reasons. First, all ingroup taxa are within the range of distances over which percent sequence divergence is approximately linear with time (12°C; Springer, Davidson, and Britten 1992). Second, although distances to the outgroup are much greater (33.0°C), our conversion of T_m to T_mH-C should further reduce compression of outgroup distances due to homoplasy. Finally, it appears that the taxa we compared

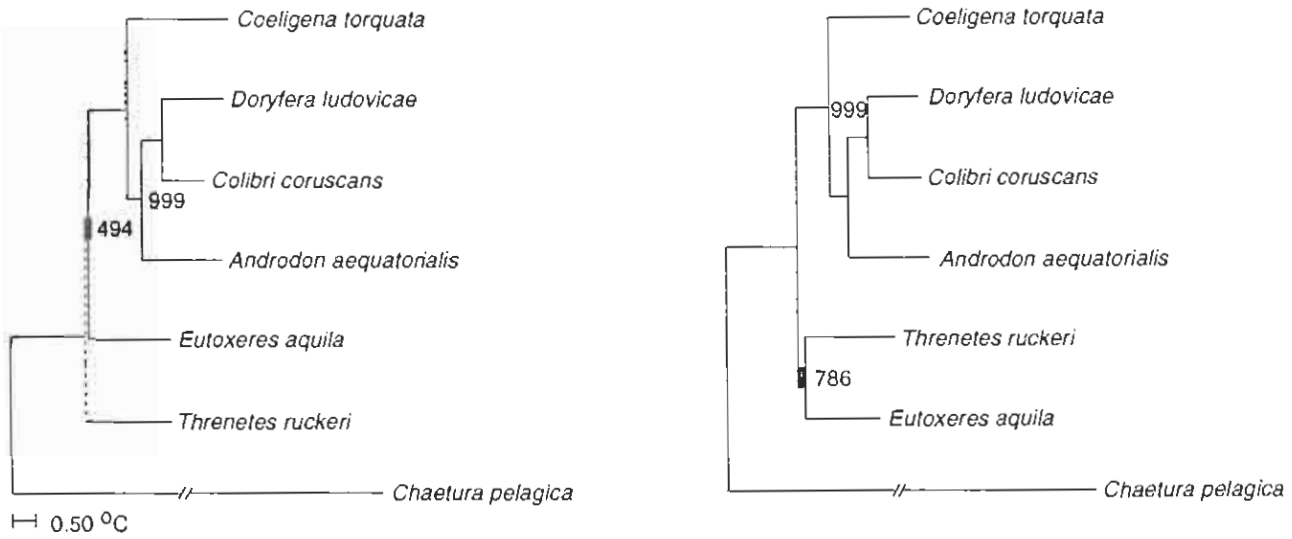

FIG. 4.—Consensus bootstrap FITCH topologies based on unsymmetrized (*left*) and symmetrized (*right*) ΔT_{α}H-C for taxa in common with Bleiweiss, Kirsch, and Matheus 1994. Branch lengths are averages over the 1,000 bootstrap pseudoreplicate trees and are drawn to scale. Dashed lines indicate nodes that collapse in jackknifing, percentages indicate support out of 1,000 bootstrap pseudoreplicate trees (if less than 100%), and gray bars indicate nodes that are not significantly different from zero length ($P \leq 0.05$).

provided us with multiple representatives from major hummingbird clades. The ultimate effect of these selections is that any potentially long branch is subdivided by the multiple representatives of that clade. Admittedly, we often were forced to adopt a typological approach to genera in order to broaden coverage. We note, however, that the actual genetic distances that separate sister genera vary widely within the phylogeny. In particular, many recognized genera (see figs. 2 and 3) are no more divergent than congeneric species (*Coeligena*). Therefore, our choices actually define a continuum of genetic divergences and do not simply reflect artifacts based on a preconceived taxonomic classification.

Several empirical tests of the stability of DNA hybridization topologies to taxonomic sampling are provided by the present study. For reasons related to those given above, it has been observed previously that inclusion of either distant or near outgroups may distort ingroup topologies, especially when short internodes occur among ingroup taxa (Marshall 1991; Kirsch, Lapointe, and Foeste 1995). Although all these conditions obtain for our phylogeny, we recovered exactly the same branching arrangements when the most distant outgroup, the swift, was removed (unpublished data). Moreover, the present study duplicates the exact same relationships among a subset of seven taxa common to our earlier comparisons among nine apodiformes (Bleiweiss, Kirsch, and Matheus 1994): the distant outgroup swift (*Chaetura pelagica*), two of the four hermits (*Eutoxeres aquila* and *Threnetes ruckeri*), and four nonhermits (*Androdon aequatorialis, Colibri coruscans, Doryfera ludovicae,* and *Coeligena torquata*). This comparison is not a fully independent test because the present study drew from the same set of extracts/individuals for five of the species (all except *Chaetura pelagica* and *Colibri coruscans*) used in our earlier study. However, we have shown previously that variance contributions by individuals and extracts are significantly less than those contributions by different tracer preparations (Bleiweiss and Kirsch 1993*b*), which were redone for the present study. Again, this subset of relationships does not change with exclusion of the outgroup swift (unpublished data).

To provide an even more severe test of taxonomic sampling bias, we also examined the consequences of reducing the 27 × 27 matrix to those seven taxa held in common with our earlier study (Bleiweiss, Kirsch, and Matheus 1994). This pruning should exacerbate instability caused by the presence of divergent singletons, because the remaining hermits in the 7 × 7 matrix comprise single representatives of the two most divergent clades in that putative group; and the remaining nonhermits represent only two of the six principal lineages. Despite this severe reduction, both unsymmetrized and symmetrized topologies agree with the results for the 9 × 9 and 27 × 27 matrices except in that *Eutoxeres* forms the sister group to the nonhermits in the unsymmetrized FITCH tree (fig. 4). However, this discrepancy depends on a short internode that receives low bootstrap support and collapses under jackknifing. Coincidentally, the internode that determines placement of the two hermits fails the branch-length test for topologies based on either symmetrized or unsymmetrized data (see fig. 4). This poor resolution at the base of the 7 × 7 matrix suggests that our earlier comparison among nine taxa comprising one swift, four hermits, and four nonhermits was almost the minimum sample needed to address the hermit–nonhermit division. In any case, the results with the 7 × 7 matrix are consistent with those of both the 9 × 9 and the 27 × 27 matrices, which in turn agree on all aspects of branching among shared taxa.

We view the general consistency of these analyses as remarkable given the almost four-fold range of matrix sizes. Inconsistent results may obtain, but only under the combined effects of sparse sampling, marked rate variation, and matrix characteristics that do not conform to the symmetry properties expected of distance data.

Thus, DNA hybridization phylogenies of taxonomically rich clades, and/or those that have no near relatives, need not give misleading results and are repeatable. This gives us confidence that the framework for hummingbird phylogeny provided by the present study will continue to hold up even for a broader suite of comparisons than the ones presented here. Moreover, evidence for the instability of analyses on unsymmetrized data is helpful in the present case also for interpreting discrepancies between topologies based on unsymmetrized and symmetrized data for the 27 × 27 matrix (see below).

All DNA hybridization studies also must consider potential inaccuracies and imprecisions in replicate measures. Although the three replicates per taxon that we employed in this study are fewer than those used in most recent studies, two factors give us confidence in the support our data provide even for short internodes in the tree. First, the tablewide average within-cell standard deviation for T_m in our matrices is low relative to that observed in most other such studies (Bleiweiss and Kirsch 1993*b*; Sheldon and Winkler 1993; Bleiweiss, Kirsch, and Matheus 1994), suggesting that we achieved high precision because the chances of obtaining such nearly identical measurements seem slim if the parametric variance was greater. This high precision obtains even in the face of a sampling scheme designed to obtain robust variance estimates. Second, the sheer size of our complete matrix increases the actual number of replicate distances measured through internal nodes. Thus, although any particular one-way comparison provides only three replicates, support for any given node is based on all of the pairwise comparisons that pass through it, which increase as the square of the number of taxa. Finally, our data are highly additive and, therefore, conform to one special assumption of least-squares tree-building algorithms.

Despite these characteristics of our data, we note several areas of uncertainty in our phylogeny. The first and most crucial for understanding hummingbird phylogeny is the short internode that determines the pattern of branching among the three principal derived nonhermit clades: the two Andean lineages and the emeralds plus bees. The behavior of this internode highlights the importance of subjecting data to multiple treatments and validation tests because different arrangements are obtained for symmetrized and unsymmetrized data, which themselves receive unequal support from different validation tests. There are three possible interpretations of our results. One is to consider the extreme shortness of the internode, and its near-zero length in the tree based on unsymmetrized data, as a biological reality. That is, that the divergence between these three clades approximates a star pattern of divergence. A more conservative interpretation is that we simply failed to resolve this exceptionally short internode. Potentially, the sheer number of reciprocal distances running through this deep node could lend high support to alternative arrangements despite inaccuracies in the data. This phenomenon may be in evidence even for the terminal node that associates the long-tailed Andean taxa, where bootstrap support also differs considerably between unsymmetrized and symmetrized data. Perhaps the most compelling evidence for systematic bias is the fact that these two nodes behave in opposite ways under symmetrization; the internal node receives increased support, while the external node receives decreased support.

Alternatively, there are substantial empirical and theoretical reasons to favor the arrangement indicated by analyses on symmetrized data. Most obviously, only the symmetrized topology passes all three validation tests, whereas the unsymmetrized topology fails the branch-length test (it has statistically zero length) and receives low bootstrap support (approximately 68% compared to over 96% for the symmetrized arrangement of the Andean clades). This difference is in fact to be expected because symmetrization reduces inconsistencies in the matrix and, in this case, also appears to lengthen the branches. These properties are reflected in the generally higher support for relationships over the entire topology based on symmetrized as compared to unsymmetrized data. Indeed, as discussed above, symmetrized and unsymmetrized topologies for the reduced 7 × 7 matrix behave in entirely parallel ways. In that case, ample ancillary evidence also favors the arrangement based on symmetrized data. Finally, there is also the theoretical consideration that symmetrization modifies relationships among distances so that they more closely adhere to the additivity assumption of least-squares tree-building algorithms. For all of these reasons, therefore, we propose that the placement of the *Eriocnemis luciani–Heliodoxa jacula–Coeligena* spp. clade basal to coquettes and their allies is likely to prove correct.

The other areas of irresolution or weak validation involve a few terminal associations (*Chlorostilbon mellisugus* within emeralds, *Myrtis fanny* within bees). These problematic branches are perhaps easier to understand as the simple consequence of too few replicates. Unlike for deeper nodes in the tree, support for these associations is influenced much more by the few replicates for each taxon. Hence, we are not surprised that short internodes receive generally weaker support when located near the tips of the tree. Thus, the majority of the phylogeny provides extremely well-supported hypotheses that define subfamilies, the major subgroups of nonhermit hummingbirds, and many relationships within these latter clades.

Principal Hummingbird Clades

The expanded comparisons of this study add considerably to an understanding of cladistic structure within the diverse nonhermits. For the reasons given above, we believe that our framework for the principal lineages will withstand additional comparisons. Here we discuss in greater detail each of these clades.

Hermits–Nonhermits

Although the swift provides only one outgroup for placement of the root among hummingbirds, our broadened comparisons among the nonhermits lend support

to earlier evidence based on allozymes (Gill and Gerwin 1989), DNA hybridization (Sibley and Ahlquist 1990; Bleiweiss, Kirsch, and Lapointe 1994), and morphology (Zusi and Bentz 1982) for the traditional distinction between hermits (*Eutoxeres aquila* and *Threnetes ruckeri*) and nonhermits (remaining taxa). These two groups remain the deepest division among extant hummingbirds, and evidence from our more inclusive study makes it less likely that some unsampled extant taxa diverged prior to these two clades. Although the present study includes only two of the five traditionally recognized hermit genera, the studies cited above are inclusive of all five genera. Thus, the hermit/nonhermit dichotomy appears to be consistent with all available evidence. The present study also reaffirms earlier evidence that certain taxa sometimes placed with hermits because of plumage and behavior (*Androdon aequatorialis* and *Doryfera ludovicae*) belong among the nonhermits. Indeed, these two hermit-like forms are even more distant cladistically than they appeared to be in our earlier study, supporting our earlier contention (Bleiweiss, Kirsch, and Matheus 1994) that their similar plumages are parallel or convergent, not only on true hermits but on each other.

Earliest Branch of Nonhermits: Mangoes and Their Relatives

The present study also supports our previous results associating *Androdon aequatorialis*, *Colibri coruscans*, and *Doryfera ludovicae* to the exclusion of *Coeligena torquata* (Bleiweiss, Kirsch, and Matheus 1994). However, our earlier comparisons among nonhermits were limited to these four taxa, so we could not determine their relative branching order in the subfamily. Our expanded comparisons not only recover the exact same relations among these four taxa (figs. 2–4), but also amplify the earlier results in several important ways. Most notably, *Androdon aequatorialis*, *Doryfera ludovicae*, and *Colibri coruscans*, along with *Eulampis holosericeus* and *Heliothryx barroti*, evidently comprise a monophyletic clade that defines the first branch among nonhermits. In addition, the greater density of taxonomic sampling among members of this clade reveals some surprising sister taxa that differ greatly in bill and plumage form. Thus, *Androdon aequatorialis* and *Heliothryx barroti* are paired in all analyses, even though the former has a dull hermit-like plumage and a long bill whereas the latter has striking white and iridescent green plumage and a short, laterally compressed bill. More generally, neither of the dull-colored forms (*Doryfera ludovicae* and *Androdon aequaltorialis*), nor those with distinctive iridescent green plumage with purple auricular patches (*Heliothryx barroti* and *Colibri coruscans*) are nearest relatives in this assemblage. On the other hand, all five taxa share bill serrations or "teeth," developed in each to varying degrees (see table 1 in Ornelas 1994). Thus, the extreme elaboration of the feature that gives *Androdon* its common name, tooth-billed hummingbird, simply reflects a character that is less developed among its relatives (unpublished data).

Andean Clades: Brilliants and Coquettes

The two branches succeeding the mangoes and their relatives include largely Andean-associated forms: the brilliant clade, composed of several highly polytypic genera (*Eriocnemis*, *Heliodoxa*, and *Coeligena*), and the coquette clade, composed of the thorntails (*Popelairia conversii*) and their high-Andean relatives (*Oreotrochilus chimborazo*, *Lesbia victoriae*, and *Aglaiocercus coelestis*). The interrelationship of these two lineages depends on a short internode that presents different arrangements depending on whether the data are symmetrized. As summarized above, we believe that the various lines of evidence favoring the arrangement based on symmetrized data are compelling. Thus, we propose that the clade of brilliants and their relatives diverged prior to the coquettes and their allies. Even so, several important insights into relationships among Andean-associated forms are evident irrespective of the exact branching order of these two clades.

One of our more important discoveries pertains to the basic phylogenetic structure of hummingbird assemblages in the Andes, the region where the family attains its highest diversity. Although many Andean species appear to be close relatives, the DNA hybridization evidence suggests that principal Andean groups fall into two genetically very distinct clades separated by an average ΔT_mH-C of over 6°C. Another issue that can be addressed with our results is whether the traditional coquette genera (*Popelairia*, *Lophornis*, and *Discosura*) should be placed in their own subfamily, as suggested by Ridgway (1911). Superficially, all three of these genera form a compact group of diminutive but highly ornamented forms that Ridgway separated from other hummingbirds based on modifications to the nasal operculum and primaries, and on their unique white to buff rump band. Subfamily status for this putative group could be justified if (any one of) its members were a sister group to hermits or nonhermits, or to all hummingbirds. Although the monophyly of *Popelairia* with *Lophornis* and *Discosura* could not be addressed with available material, our results are inconsistent with subfamily designation because *Popelairia conversii* is nested within a derived clade of nonhermits. Indeed, this placement reveals that the peculiar ornaments that might distinguish the traditional coquette genera from other hummingbirds are actually echoed in their Andean relatives. Thus, the thorntails (*Popelairia*) have long and wiry tail feathers, whereas the typically Andean sylphs (*Aglaiocercus*) and trainbearers (*Lesbia*) have long tail streamers.

Given the high taxonomic diversity in Andean hummingbird communities, both of the Andean clades revealed by our analyses are probably indicative of much larger assemblages. This view is supported by the magnitude of genetic separation between subclades within the two lineages. For example, over 3°C distinguishes *Popelairia conversii* from its high-Andean relatives. One intriguing candidate that may subdivide the branch between these two subclades is the enigmatic

monotypic genus *Heliactin*, another tiny species with head ornaments reminiscent of those of *Lophornis*, as well as an ample white tail and white underparts similar to those present in *Oreotrochilus chimborazo* among *Popelairia*'s high-Andean relatives. The somewhat shorter distances among genera in the brilliant clade nevertheless indicate considerable separation among these common Andean forms, suggesting that they, too, may be linked by other taxa we did not sample. These interrelationships remain to be determined.

Emeralds and Allies

Typical of the North American trochilofauna are numerous species of emeralds (*Amazilia* etc.), tiny bee-like forms, and an odd assortment of larger taxa (*Lampornis clemenciae, Eugenes fulgens*). Our data indicate that all of these comprise a single lineage, suggesting that the majority of North American hummingbirds belong to a monophyletic radiation. Emeralds themselves would qualify as a major radiation within hummingbirds simply by inclusion of the genus *Amazilia*, which as currently defined comprises upward of 30 species (Monroe and Sibley 1993). In contrast to the largely South American highland distribution of many Andean genera, members of the emerald clade are more widely distributed across various high-/and low-elevation habitats in both North and South America as well as in the Caribbean (*Chlorostilbon* and *Orthorhyncus*). On the other hand, the traditional emerald genera *Amazilia* and *Chlorostilbon* are morphologically homogeneous, comprising numerous medium-sized species with iridescent green plumage and slightly decurved bills of moderate length. Our results serve to further characterize the emerald radiation by revealing the extraordinary variety of forms in this clade. This broader suite of genera includes ones with elaborate head ornaments (*Orthorhyncus*) or prominent blue or violet markings (*Campylopterus, Thalurania*). The sister relationship of the diminutive and short-billed *Orthorhyncus cristatus* and very large and curve-billed *Campylopterus villaviscensio* is especially remarkable given the morphological uniformity otherwise found among traditional emerald genera.

While our data place such characteristic emerald genera as *Chlorostilbon* and *Amazilia* in the same larger clade, they also indicate that typical green-colored taxa are not monophyletic within this larger assemblage. All bootstrap and jackknife analyses support a sister relationship between the green and rufous *Amazilia tzacatl* and green and violet *Thalurania colombica* to the exclusion of the green-colored *Chlorostilbon mellisugus*. Exact placement of *Chlorostilbon mellisugus* within the emeralds differed for analyses on unsymmetrized and symmetrized data, but its position as the first branch among the five taxa in the clade, as indicated by symmetrized data, was supported strongly by bootstrap and jackknife validation tests. Additional comparisons should serve to clarify *Chlorosilbon*'s placement, which bears directly on the historical significance of green plumage among emeralds and whether it is pleisiomorphic or has evolved multiple times.

Mountain-Gems and Bees

The sister group to emeralds includes two distinct lineages. One is composed of the mountain-gem *Lampornis clemenciae* and its sister taxon, the monotypic genus *Eugenes fulgens*. Unlike most members of the previously described clades, these genera are confined to North America and are the only two large-bodied species that regularly breed north of the Mexican border. The large size in combination with a brilliant violet crown and green gorget of male *Eugenes fulgens* are reminiscent of some members of the Andean genus *Heliodoxa*, which has led some to suggest that *Eugenes fulgens* might belong in that genus (e.g., Zimmer 1951; Johnsgard 1983, p. 139). Our results clearly contradict this hypothesis by demonstrating the distant separation of *Heliodoxa jacula* and *Eugenes fulgens*. The special association of mountain-gems and *Eugenes fulgens* is all the more intriguing because these two, in turn, are the sister group to the principal clade of hummingbirds found in the United States, the diminutive bees. Thus, all of the hummingbirds that regularly breed north of Mexico appear to be surprisingly close relatives. Although quite different in size, the association of mountain-gems and bees groups together two clades in which males typically have well-developed iridescent throat patches, or gorgets.

Our data support monophyly for the bees, and they distinguish distinct temperate North American (*Archilochus colubris*) and tropical (*Myrtis fanny, Acestrura mulsant*, and *Philodice mitchellii*) subclades. In addition, the different genera appear to be quite similar at the genetic level, as the distance between even members in the two most distinct clades is less than 2.0°C.

Comparisons With Other Studies

Morphology

Zusi and Bentz (1982) divided hummingbirds into four groups based on variation in the wing muscle tensor propatagialis pars brevis (TPB; types I–IV, table 1). The clades identified by our DNA hybridization study correspond to these groupings with the caveat that the type III condition is paraphyletic with respect to type IV (table 1). This concordance is highlighted by mutual support for specific relationships (e.g., early divergence for *Heliothryx barroti*, later divergences for *Popelairia conversii* and *Campylopterus villaviscensio*) inconsistent with the standard linear arrangement of hummingbirds (table 1). Additional comparisons will be needed to confirm monophyly of the type IV clade because we examined only *Acestrura* among the three genera Zusi and Bentz identified with this condition. Given the limited scope of available molecular hypotheses of hummingbird relationships, we note that TPB can serve as a useful guide for selecting appropriate comparisons in future molecular studies.

DNA Hybridization

Sibley and Ahlquist's (1990) work comparing 20 hummingbird species is the only other published molecular study of broad relationships among nonhermits. In contrast to our experimental design, these authors labeled only two nonhermit taxa, obtained few replicates, and then used UPGMA to cluster on distances. Their choice to measure distances with raw measures of T_{50}H compounds the problem of few replicates because of the high experimental error associated with the normalized percentage of hybridization incorporated into this index. As Sibley and Ahlquist did not apply any validation methods to their topologies, support for their phenogram cannot be assessed. Nevertheless, our FITCH tree and their topology agree to a considerable extent about deeper phylogenetic structure among hummingbirds common to both studies. As did we, they obtained a succession of clusters including hermit genera (*Eutoxeres, Phaethornis, Threnetes,* and *Glaucis*), basal nonhermits (*Androdon* and *Colibri*), two distinct Andean clades (represented by *Lesbia* spp. and *Coeligena*), and emeralds (*Chlorostilbon, Campylopterus,* and *Amazilia*); they did not include representatives from coquettes, mountain-gems, or bees, among others. Thus, our studies agree on many of the basic groupings among hummingbirds, including surprising associations such as inclusion of *Campylopterus* and *Thalurania* among the emeralds. Sibley and Ahlquist's results also provide preliminary support for some associations we could not resolve. Thus, they found that the two unlabeled *Amazilia* species were closest to the labeled third, tentatively indicating monophyly for a portion of this species-rich genus.

The agreement between studies is surprising given obvious limitations in Sibley and Ahlquist's methods. Possible explanations for the unexpected agreement may stem from several sources. One is that their two labeled taxa, *Coeligena bonapartei* and *Amazilia tzacatl*, are indicated to be members of relatively distal (far from the root) clades in our study. Given limited one-way comparisons, distances measured from proximal (closer to the root) to more distal clades will be less informative than the converse. The reason for this is that comparisons from members of proximal to more distal branches must pass through the node shared by the common ancestor of all taxa in the more distal clade. Thus, differences in distances to these taxa reflect variation only in rate and in experimental error. On the other hand, taxa in the distal clade may join proximal branches at different levels of the tree and, therefore, include more information about cladistic structure. Of course, any such structure could be swamped by large amounts of experimental error. For T_{50}H, this error is contributed largely by NPH. This error may have been minimized in Sibley and Ahlquist's study because NPH among even the most divergent hummingbirds exceeds 85%. Thus, T_{50}H measures approximated closely those obtained with T_m or our regressed T_mH-C.

Sibley and Ahlquist resolved no structure within those larger groupings from which they did not label taxa. However, our studies differ for some relationships within the clades of the labeled taxa. Whereas we found that *Amazilia* and *Thalurania* were sister taxa exclusive of *Chlorostilbon*, Sibley and Ahlquist's phenogram indicates monophyly for the two traditional emerald genera, *Chlorostilbon* and *Amazilia*, with *Thalurania* as an earlier branch. Coincidentally, these relationships depend on short internodes, some of which were unstable in our study, e.g., placement of *Chlorostilbon*. For the reasons mentioned earlier, a larger number of replicates (lacking in both our and Sibley and Ahlquist's studies) would presumably aid in resolving these closely spaced and near-terminal branches.

Taxonomy

Generic Classification

Numerous hummingbird genera are based on bill and plumage characters that are used also to distinguish different hummingbird species (Elliot 1879; Boucard 1895; Taylor 1909; Ridgway 1911). Thus, it has long been suspected that the many hummingbird genera (Morony, Bock, and Farrand 1975) do not reflect underlying levels of genetic divergence or cladistic relationship (Mayr and Short 1970). In fact, our distance data identify several monophyletic clades whose constituent genera are no more divergent genetically than are the congeneric *Coeligena* species: the trio of high Andean taxa (*Oreotrochilus chimborazo, Aglaiocercus coelestis,* and *Lesbia victoriae*) that form the sister group to the thorntails, and the clade of tropical bees (*Myrtis fanny, Acestrura mulsant,* and *Philodice mitchellii*). Our data could serve as justification for lumping such genera into more inclusive monophyletic taxa. On the other hand, genetic divergence between some monotypic genera (*Orthorhyncus* and *Eugenes*) and their respective sister groups is quite large, arguing that these genera should be retained pending evidence to the contrary. Thus, while many nonhermit genera are poorly differentiated at the genetic level, judgments as to generic taxonomy will have to be made on a case-by-case basis. Presumably, decisions about generic taxonomy may become ambiguous when a greater density of comparisons is available, as a complete gradation of genetic distances and degrees of morphological divergences may be found to exist.

Linear Sequence

Linear classifications typically place what are considered the most primitive taxa at the head of the list and then proceed through more derived groups. In cladistic terms, this usually amounts to beginning with the basal taxa and proceeding with successive branches in a largely pectinate tree. Although we do not here propose any formal taxonomic changes, the following relationships implied by our phylogeny could serve as the basis for revisions to the traditional linear ordering of hummingbird taxa (Peters 1945; Monroe and Sibley 1993; compare with table 1). All members of the man-

go clade should be placed at the beginning of the nonhermit sequence. As a deeper branch within this group, *Eulampis holosericeus* should precede *Androdon aequatorialis* and its sister taxon *Heliothryx barroti*, which should be moved from near the end of the standard sequence. The Andean genera *Eriocnemis*, *Heliodoxa*, and *Coeligena* should be placed together, as should coquettes and their Andean relatives *Oreotrochilus chimborazo*, *Aglaiocercus coelestis*, and *Lesbia victoriae*. The placement of these two clades within the sequence will depend on resolution of their branching order. However, the emeralds should follow both Andean clades and include pairings of *Amazilia tzacatl* and *Thalurania colombica* and of *Campylopterus villaviscensio* and *Orthorhyncus cristatus*. These taxa, in turn, should be followed by the mountain-gems *Lampornis clemenciae* and *Eugenes fulgens*. On the other hand, current placement of the bees at the end of the sequence is consistent with the terminal location of their branch. Given the many surprising associations revealed by our comparisons among just 26 hummingbird taxa, broader sets of comparisons will undoubtedly suggest many more intriguing relationships.

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NAOYUKI TAKAHATA, reviewing editor

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APPENDIX 1

Summary of Specimens Used, with Each Individual Identified by its DNA Extract Number

Threnetes ruckeri. Centro Cientifico Rio Palenque, 56 km SW of Santo Domingo de los Colorados, on Rio Babo, Provincia de Los Ríos (1277, 1278).

Eutoxeres aquila. Encampamento de CODESA, 21.6 road km from Pedro Vicente Maldonado, Provincia de Pichincha, Ecuador (1162, 1163, 1401).

Androdon aequatorialis. Encampamento de CODESA, 21.6 road km from Pedro Vicente Maldonado, Provincia de Pichincha, Ecuador (1397, 1398, 1436).

Doryfera ludovicea. Below Hacienda Santa Rosa on Río Cinto, Provincia de Pichincha, Ecuador (1353, 1354, 1438).

Campylopterus villavicencio. Carratera Hollín-Loreto, 54 km E of Narupa, Provincia del Napo, Ecuador (1877, 1878).

Colibri coruscans. Calle Gonzalo Pizarro, 2.0–2.5 km from Via Interoceania, Barrio Churo Loma, Tumbaco, Provincia de Pichincha, Ecuador (1846, 1847); Ridge above Hacienda San René, Mindo, Provincia de Pichincha, Ecuador (1848).

Eulampis holosericeus. Guana Island, British Virgin Islands (1281, 1282, 1850).

Orthorhyncus cristatus. Guana Island, British Virgin Islands (1849, 1869, 1870).

Popelairia conversii. Km 13 from Y between Mindo and Los Bancos, Old Mindo Road, Provincia de Pichincha, Ecuador (2024, 2025, 2026).

Chlorostilbon mellisugus. Hacienda Georgia, 2.0 km from La Via Tumbaco, Provincia de Pichincha, Ecuador (1943); Calle Gonzalo Pizarro, 2.0–2.5 km from Via Interoceania, Barrio Churo Loma, Tumbaco, Provincia de Pichincha, Ecuador (1944, 1945).

Thalurania colombica. 1.0 km from CODESA camp below Cooperativa Salsedo Lindo, Encampamento de CODESA, 21.6 road km. From Pedro Vicente Maldonado, Provincia de Pichincha, Ecuador (1160, 1838, 1839).

Amazilia tzacatl. Hacienda San René, Mindo, Provincia de Pichincha, Ecuador (1863, 1864, 1865).

Lamporuis clemenciae. Harb Martyr Road, 1.0 km W of Southwest Research Station, Chiricahua Mountains, Cochise County, Arizona, United States (1836, 1837, 1838).

Heliodoxa jacula. Hacienda Santa Isabel on Old Road to Chiriboga, 2.6 km above Toachi at Puenta across Río Pilatón, Provincia de Pichincha, Ecuador (2030, 2031).

Eugenes fulgens. Herb Martyr Road, 1.0 km W of Southwest Research Station, Chiricahua Mountains, Cochise County, Arizona, United States (1840, 1841, 1842).

Oreotrochilus chimborazo. Road to refugio de la Defensa Civil, Guagua Pichincha, Provincia de Pichincha, Ecuador (1843, 1844, 1845).

Coeligena wilsoni. Estacion Cientifica Río Guajalito, Las Palmas, Road to Chiriboga, Provincia de Pichincha, Ecuador (1874, 1875, 1876).

Coeligena torquata. Below Hacienda Santa Rosa on Río Cinto, Provincia de Pichincha, Ecuador (1399, 1400).

Eriocnemis luciani. Hacienda Mi Cielo, Quito, Provincia de Pichincha, Ecuador (1871, 1872, 1873).

Lesbia victoriae. Bosque Protector Pichinca, 2.0 km from Avenida Occidental, Provincia de Pichincha, Ecuador.

Aglaiocercus coelestis. Ridge above Hacienda San René, Mindo, Provincia de Pichincha, Ecuador (1940, 1941, 1942).

Heliothryx barroti. Centinella de Guayllabamba, above Río Guayllabamba, Provincia de Pichincha, Ecuador (2045); 1.0 km from CODESA camp below Cooperativa Salsedo Lindo, Encampamento de CODESA, 21.6 road km. From Pedro Vicente Maldonado, Provincia de Pichincha, Ecuador (2046).

Phlodice mitchellii. Below Hacienda Santa Rosa, Río Cinto, New Road to Mindo, Provincia de Pichincha, Ecuador (2035); Hacienda San René, at Puenta across Río Nambilla, Mindo, Provincia de Pichincha, Ecuador (2036); 15 km from Colegio Ecuatoriano on road to Y, Mindo, Provincia de Pichincha, Ecuador (2037).

Archilochus colubris. Trout Lake Biological Station, Highland State Forest, Vilas County, Wisconsin, United States.

Myrtis fanny. Calle Gonzalo Pizarro, 2.0 km from Via Interoceania, Barrio Churo Loma, Tumbaco, Provincia de Pichincha, Ecuador (2032, 2033); Cooperativa San Jose, Tumbaco, Provincia de Pichincha, Ecuador (2034).

Acestrura mulsant. Hacienda Vera Cruz, Barrio Churo Loma, Tumbaco, Provincia de Pichincha, Ecuador (2027, 2028, 2029).

Chaetura pelagica. Town of McFarland, Dane County, Wisconsin, United States (2038, 2039).

NOTE.—Voucher specimens deposited as study skins, spirit specimens, or skeletons in collections of the University of Wisconsin Zoological Museum or Museo Ecuatoriano de Ciencias Naturales.

APPENDIX 2

Summary Statistics[a] for Unsymmetrized ΔT_mH-C Values[b]

	LampC[c]	ThalC	AglaC	CoelW	EriaL	EulaH	ColiC	EugeF	AcesM	ArchC	MyrtF	PhilM	AmaxT	CamyV	AndrA	LeahV	DoryL	OreoX	HeliJ	HeliB	ChloM	CoeiT	PapeC	OrthC	ThreR	HutoA	ChaeF
Lamprornis	86.18	4.36	6.41	6.10	6.72	8.73	7.26	2.74	3.57	2.85	6.05	3.38	4.30	6.52	8.56	5.80	8.59	6.38	6.44	9.89	6.86	7.39	7.00	6.04	9.98	10.18	33.19
clemenciae	0.22/3	0.11/3	0.04/3	0.22/3	0.61/1	0.22/3	0.20/3	0.33/3	0.14/3	0.18/3	0.28/3	0.16/3	0.04/3	0.19/3	0.22/3	0.51/3	0.04/2	0.11/3	0.02/3	0.08/3	0.61/3	0.66/3	0.29/3	0.15/3	0.16/3	0.21/3	0.62/3
Thalurania	6.22	84.02	6.98	6.32	7.24	8.80	7.46	3.98	4.34	3.71	6.85	4.12	3.66	4.05	8.64	6.61	9.07	6.56	6.61	10.30	4.21	6.28	7.63	3.91	10.24	10.09	32.59
colombica	0.23/3	0.10/3	0.46/3	0.51/3	0.22/3	0.59/3	0.29/3	0.65/3	0.15/3	0.46/3	0.63/3	0.20/3	0.23/3	0.21/3	0.66/3	0.60/2	0.66/3	0.17/3	0.56/3	0.24/3	0.15/3	0.18/3	0.68/3	0.18/3	0.20/3	0.17/3	0.44/3
Aglaiocercus	6.22	6.66	83.21	6.04	6.71	8.16	7.18	6.05	6.66	5.56	6.76	6.29	6.71	6.76	8.45	2.37	8.62	2.21	6.33	9.56	7.21	7.18	5.34	6.45	9.85	10.08	33.18
coelestis	0.27/3	0.20/3	0.47/2	0.30/3	0.19/3	0.32/3	0.80/3	0.50/3	0.06/3	0.15/3	0.06/3	0.38/3	0.24/3	0.39/3	0.11/3	0.26/3	0.32/3	0.14/3	0.21/3	0.02/2	0.09/3	0.70/3	0.29/3	0.06/2	0.23/3	0.44/3	0.64/3
Coeligena	6.08	6.61	6.35	83.81	6.66	8.33	6.71	6.01	6.23	5.59	6.91	6.41	6.62	6.69	7.88	6.65	8.05	6.20	6.16	9.36	7.17	2.77	6.57	6.65	10.01	9.65	32.60
wilsoni	0.37/3	0.03/3	0.26/3	0.09/3	0.13/3	0.26/3	0.30/3	0.77/3	0.23/3	0.22/3	0.44/3	0.27/3	0.19/3	0.12/3	0.33/2	0.66/3	0.14/3	0.16/3	0.22/3	0.06/3	0.12/3	0.18/3	0.43/3	0.66/3	0.63/3	0.09/3	0.32/3
Eriocnemis	5.70	6.32	6.41	3.99	83.23	7.88	7.00	5.92	6.16	5.26	6.87	6.03	6.21	6.28	7.77	5.54	7.90	6.00	6.22	9.09	6.54	6.39	6.49	6.20	10.07	9.16	32.10
luciani	0.26/3	0.09/3	0.24/3	0.33/2	0.18/3	0.51/3	0.28/3	0.32/3	0.15/3	0.33/3	0.37/3	0.35/3	0.37/3	0.17/3	0.31/3	0.37/3	0.12/3	0.33/3	0.18/3	0.07/3	0.23/3	0.30/3	0.02/3	0.38/3	0.23/3	0.67/3	0.83/3
Eulampis	8.77	9.01	8.83	8.51	9.16	83.32	6.42	8.80	8.96	8.28	9.41	9.06	9.53	9.26	7.18	9.03	7.64	8.83	9.07	8.32	9.88	9.39	9.42	9.21	10.33	9.96	32.59
holosericeus	0.29/3	0.27/3	0.12/3	0.36/3	0.34/3	0.32/3	0.11/3	0.44/3	0.17/3	0.16/3	0.64/3	0.35/3	0.22/3	0.05/3	0.10/3	0.44/3	0.36/3	0.40/3	0.04/3	0.18/3	0.22/3	0.38/3	0.27/3	0.56/2	0.25/3	0.23/3	0.68/3
Colibri	8.14	8.55	8.30	8.08	8.69	7.72	83.06	8.09	8.84	7.69	8.78	8.69	8.97	8.59	6.80	8.53	5.04	7.92	8.41	8.26	9.54	8.97	8.78	8.79	9.54	9.41	32.62
coruscans	0.25/3	0.09/3	0.42/3	0.33/3	0.17/3	0.67/3	0.70/3	0.19/3	0.54/3	0.25/3	0.18/3	0.36/3	0.41/3	0.11/3	0.26/3	0.37/3	0.23/3	0.06/3	0.39/3	0.19/3	0.34/3	0.23/3	0.66/3	0.61/3	0.46/3	0.08/3	0.26/3
Eugenes	2.90	4.22	6.65	6.17	6.75	8.69	7.29	83.92	3.41	2.53	3.76	3.20	4.25	4.16	8.28	6.93	8.70	6.33	6.70	9.65	4.02	7.07	7.30	3.61	10.30	10.00	32.53
fulgens	0.08/3	0.17/3	0.36/3	0.19/3	0.16/3	0.10/3	0.50/3	0.26/3	0.06/3	0.18/3	0.17/3	0.10/3	0.46/3	0.15/3	0.32/2	0.82/3	0.25/3	0.47/3	0.53/3	0.13/3	0.52/3	0.46/3	0.24/1	0.41/3	0.30/3	0.13/3	1.15/3
Acestrura	3.58	4.29	6.89	6.52	7.05	8.89	7.28	3.15	84.03	1.21	1.03	0.56	4.55	6.69	8.83	7.11	9.08	6.68	6.89	10.17	6.67	7.16	7.09	6.66	10.50	10.27	32.68
mulsant	0.23/3	0.16/3	0.50/3	0.32/3	0.35/3	1.07/3	0.71/3	0.06/3	0.09/3	0.16/3	0.18/3	0.35/3	0.18/3	0.02/3	0.41/3	0.41/3	0.44/3	0.22/3	0.24/3	0.22/3	0.56/3	0.56/3	0.22/3	0.73/3	0.22/3	0.30/3	0.65/3
Archilochus	3.53	4.35	7.07	6.35	7.19	8.74	7.39	3.02	2.15	83.76	1.99	1.88	4.47	6.30	8.27	6.56	8.79	6.58	6.69	9.82	6.40	7.12	7.62	6.25	10.25	10.45	32.58
colubris	0.23/3	0.15/3	0.51/3	0.20/3	0.30/3	0.08/3	0.19/3	0.31/3	0.25/3	0.27/3	0.17/3	0.17/3	0.23/3	0.42/3	0.56/3	0.51/3	0.33/3	0.46/3	0.35/3	0.35/3	0.36/3	0.21/3	0.74/3	0.64/3	0.38/3	0.77/3	0.32/3
Myrtis	3.58	4.60	6.78	6.78	7.65	8.76	7.79	3.10	0.61	1.35	84.31	0.63	4.60	6.47	8.71	6.31	8.66	6.72	6.87	10.20	6.86	7.20	7.23	6.18	10.46	10.33	33.28
fanny	0.18/3	0.09/3	0.69/3	0.32/3	0.27/3	0.17/3	0.23/3	0.16/3	0.18/3	0.03/3	0.10/3	0.08/3	0.13/2	0.18/3	0.52/3	0.40/3	0.10/3	0.24/3	0.23/3	0.36/3	0.21/3	0.68/3	0.28/3	0.25/3	0.08/3	0.15/3	0.18/3
Phlodice	3.39	4.61	7.08	6.73	7.17	8.18	7.70	3.31	0.49	1.06	1.22	83.76	4.39	6.55	8.35	6.32	8.74	6.64	6.70	9.92	6.59	6.99	7.21	6.11	10.24	10.28	33.18
mitchellii	0.29/3	0.11/3	0.54/3	0.23/3	0.25/3	0.57/3	0.19/3	0.12/3	0.06/3	0.18/3	0.20/3	0.24/3	0.24/3	0.31/3	0.56/3	0.26/2	0.14/3	0.22/3	0.13/3	0.26/3	0.15/3	0.03/3	0.41/3	0.07/3	0.30/3	0.38/3	0.16/3
Amazilia	4.28	3.64	6.76	6.50	6.83	8.82	7.15	3.65	4.27	3.66	4.66	4.44	83.80	4.01	8.86	6.81	8.83	6.48	6.79	10.01	4.61	7.21	7.59	3.80	10.27	10.22	32.84
tzacatl	0.32/3	0.09/3	0.24/3	0.06/3	0.25/3	0.19/3	0.12/3	0.18/3	0.35/3	0.15/3	0.07/3	0.42/3	0.09/3	0.13/3	0.17/3	0.19/3	0.46/3	0.21/3	0.05/3	0.09/3	0.22/3	0.65/3	1.00/3	0.17/3	0.78/3	0.01/2	0.84/3
Campylopterus	4.24	4.21	6.75	6.43	7.05	8.88	7.56	3.98	4.13	3.43	4.83	4.69	4.30	84.43	9.31	7.01	8.89	6.67	6.88	9.93	4.20	7.88	7.63	3.01	11.01	10.50	32.16
villaviscensio	0.11/2	0.18/3	0.01/2	0.16/2	0.02/2	0.11/2	3.56/2	0.13/3	0.25/2	0.06/2	0.10/2	0.11/2	0.13/2	0.06/2	0.30/2	0.11/2	0.31/2	0.14/2	0.07/2	0.06/2	0.28/2	0.13/2	1.13/2	0.49/2	1.10/2	0.08/2	0.09/3
Androdon	8.76	8.98	8.61	8.51	9.36	7.48	6.08	8.21	8.96	8.12	9.17	9.02	9.14	9.13	83.48	8.66	7.55	8.49	8.66	6.80	9.96	9.31	9.40	8.23	9.89	10.03	33.65
aequatorialis	0.37/3	0.11/3	0.13/3	0.20/3	0.13/3	0.12/3	3.64/3	0.38/3	0.22/3	0.19/3	0.48/3	0.77/3	0.30/3	0.21/3	0.27/3	0.50/3	0.34/3	0.14/3	0.75/3	0.50/3	0.34/3	0.91/3	0.22/3	0.60/3	0.79/3	0.90/3	9.36/3

Lesbia	6.20	6.60	3.08	6.25	6.69	8.02	7.13	6.05	6.18	5.67	7.05	6.58	6.80	6.40	7.88	83.77	8.58	1.95	6.14	9.16	6.98	6.46	5.23	7.08	10.04	10.10	32.38
victoriae	0.24/3	0.11/3	0.34/3	0.60/3	0.10/3	0.40/3	0.38/3	0.20/3	0.31/3	0.16/3	0.24/3	0.26/3	0.29/3	0.35/2	0.59/3	0.03/3	0.21/3	0.15/3	0.07/3	0.10/3	0.58/3	0.51/3	0.29/3	0.76/3	0.06/3	0.42/3	0.56/3
Coryfera	8.43	8.89	8.91	7.93	8.68	6.82	6.20	8.28	8.50	7.55	8.75	8.35	9.10	9.05	7.00	8.14	82.82	8.49	8.57	8.56	10.22	9.51	9.24	8.39	9.34	9.35	33.86
ludoviciae	0.02/3	0.04/3	0.79/3	0.28/3	0.58/3	0.14/3	0.11/3	0.19/3	0.14/3	0.67/3	0.26/3	0.38/3	0.12/3	0.09/3	0.13/3	0.34/3	0.56/3	0.56/3	0.26/3	0.69/3	0.05/2	1.12/3	0.27/3	0.70/3	0.41/3	0.29/3	0.55/3
Oreotrochilus	6.39	6.68	7.31	5.85	6.69	7.87	6.82	6.11	6.35	5.44	7.04	6.19	7.06	6.82	8.37	3.32	8.46	82.95	6.68	9.66	6.76	6.51	5.51	6.59	10.06	10.03	31.96
chimborazo	0.35/3	0.09/3	0.25/3	0.20/3	0.19/3	0.61/3	0.24/3	0.12/3	0.28/3	0.32/3	0.02/3	0.28/3	0.19/3	0.09/3	0.13/3	0.21/3	0.18/3	0.23/3	0.02/3	0.17/3	0.54/3	0.07/2	0.37/3	0.25/3	0.11/3	0.52/3	0.66/3
Heliodoxa	6.23	6.68	6.49	6.10	6.63	8.35	7.03	5.71	6.26	5.58	6.64	6.69	7.06	6.65	8.20	5.76	8.59	6.37	83.16	9.70	7.44	6.59	7.58	6.10	10.18	10.00	32.17
jacula	0.35/2	0.12/2	0.42/2	0.08/3	0.06/2	0.59/2	0.32/2	0.57/2	0.00/2	0.04/2	0.33/2	0.16/2	0.06/2	0.26/2	0.36/2	0.31/2	0.04/3	0.18/2	0.21/3	0.26/2	0.11/2	0.35/2	0.44/2	0.21/2	0.07/2	0.17/2	0.24/3
Heliothryx	9.01	8.90	9.18	8.23	9.31	7.46	6.43	8.63	9.06	7.84	9.56	9.38	9.69	9.15	5.55	9.04	7.44	8.94	9.25	83.23	9.63	9.74	10.02	8.95	9.59	9.84	32.04
barroti	0.32/2	0.57/2	0.36/2	0.62/2	0.19/2	0.09/3	0.69/2	0.06/2	0.06/2	0.21/2	0.40/2	0.31/3	0.06/2	0.31/2	0.68/2	0.63/2	0.16/2	0.68/2	0.05/2	0.25/2	0.78/2	0.51/3	0.81/3	0.32/2	0.71/2	0.28/2	0.02/2
Chlorostilbon	6.20	6.13	7.12	6.47	7.25	8.95	7.72	3.91	6.26	3.60	6.65	6.36	6.31	6.38	8.61	7.07	9.21	6.81	6.73	10.26	82.22	7.05	6.99	6.36	10.76	10.46	32.82
mellisugus	0.20/3	0.16/3	0.70/3	0.53/3	0.23/3	0.26/3	0.67/3	0.20/3	0.08/3	0.18/3	0.16/3	0.35/3	0.25/3	0.21/3	0.30/3	0.72/3	0.30/3	0.13/3	0.06/3	0.18/3	0.23/3	0.81/3	0.66/3	0.72/3	0.19/2	0.00/2	1.32/3
Coeligena	6.15	6.38	6.20	2.36	4.21	8.23	6.38	5.50	6.27	5.31	6.76	6.09	6.79	6.51	7.95	5.53	8.13	5.20	4.02	9.17	6.17	82.00	6.67	6.90	9.83	9.75	31.54
torquata	0.28/2	0.31/2	0.31/2	0.06/2	0.08/2	0.19/2	0.47/2	0.31/2	0.08/2	0.65/2	0.11/2	0.25/3	0.07/2	0.08/2	na/1	na/1	0.31/2	0.10/2	0.56/2	0.02/2	0.18/2	0.12/2	0.48/2	0.59/2	0.47/2	0.59/2	0.15/2
Popelairia	7.31	7.49	5.81	7.38	7.61	9.67	8.07	6.61	7.32	6.68	7.91	7.32	7.67	7.70	8.91	5.55	9.54	5.51	7.05	10.11	8.02	7.58	82.69	6.98	10.64	11.06	33.61
conversii	0.96/3	0.08/3	0.39/3	0.16/3	0.23/3	0.18/3	0.15/3	0.30/3	0.12/3	0.16/3	0.04/3	0.32/3	0.20/3	0.25/3	0.03/3	0.60/3	0.17/3	0.06/3	0.23/3	0.50/3	1.03/3	0.42/3	0.52/3	0.44/3	0.59/3	0.36/3	0.75/3
Orthorhyncus	6.72	6.10	6.89	6.68	7.35	9.22	7.64	6.22	6.50	3.91	6.73	6.63	6.36	3.11	8.61	6.93	9.57	6.88	6.81	10.06	6.43	7.32	7.50	82.79	10.65	10.58	33.00
cristatus	0.86/3	0.32/3	0.17/3	0.21/3	0.40/3	0.63/3	0.05/3	0.58/3	0.39/3	0.11/3	0.16/3	0.30/3	0.33/3	0.24/3	0.44/3	0.42/3	0.27/3	0.21/3	0.28/3	0.12/3	0.64/3	0.33/3	0.63/3	0.24/3	0.75/3	0.29/3	0.66/3
Threnetes	10.06	10.73	10.51	10.53	10.93	9.98	9.34	10.53	10.67	9.59	11.01	11.01	11.22	10.67	9.74	10.93	10.67	10.51	10.66	11.10	11.81	10.97	12.24	10.95	82.57	7.60	31.73
ruckeri	1.15/2	0.68/2	0.01/2	0.32/2	0.09/2	0.23/2	0.47/2	0.07/3	0.05/2	0.23/2	0.17/2	0.16/2	0.00/3	0.11/2	0.66/2	0.18/2	0.88/2	0.16/2	0.21/3	0.43/2	0.38/2	0.88/2	0.88/2	0.08/2	0.28/2	0.04/2	0.11/2
Eutoxeres	10.00	10.17	10.61	10.19	10.31	10.20	7.84	9.43	9.79	8.95	10.27	10.06	9.91	10.00	9.43	9.98	9.32	9.63	10.17	10.26	10.81	11.07	10.52	10.10	7.19	81.85	31.59
aquila	0.46/3	0.17/3	0.30/3	1.11/3	0.88/3	1.59/3	0.56/3	0.65/3	0.30/3	0.39/3	0.08/3	0.36/3	0.66/3	0.04/3	0.19/3	0.82/3	0.59/3	0.46/3	0.14/3	0.26/3	0.21/3	1.66/3	0.61/3	0.21/3	0.06/3	0.42/3	1.51/3
Chaetura	36.86	14.03	36.07	29.79	34.19	31.54	32.76	33.62	33.09	31.60	36.12	31.93	35.61	33.81	33.10	33.17	36.88	30.76	33.42	35.38	36.49	33.61	32.41	30.78	29.88	30.92	83.40
pelagica	1.06/2	2.06/2	1.08/2	1.63/2	0.95/2	0.17/2	0.09/2	0.26/2	0.04/3	0.45/2	1.09/2	0.98/2	1.68/2	0.99/2	2.35/3	3.94/2	0.41/2	0.30/2	1.87/2	0.18/2	3.12/2	1.45/2	1.17/2	0.04/2	0.44/2	0.66/3	0.07/2
Correction[c]	0.991	0.988	0.965	1.010	0.896	1.042	1.136	1.037	1.021	1.148	0.952	1.011	0.961	0.999	1.040	0.982	0.965	1.065	0.975	0.917	0.947	0.884	1.015	1.053	1.049	0.986	1.021

[a] Mean melting temperature followed by standard deviation/number of replicates. Scalar correction for percent nonreciprocity indicated at the bottom of each corresponding column. Actual melting temperatures of homologous hybrids indicated along the diagonal. The two-degree range of mean homologous melting temperatures is typical of DNA hybridization studies. Trochiline taxa are listed in the order in which their labels were run in the TED.

[b] Correlation of standard deviation with distance (df = 25): without swift, $r = 0.177$ ($P \geq 0.10$); with swift, $r = 0.425$ ($P < 0.10$) (see text).

[c] First four letters of genus plus first letter of species name.

[d] Initial row/column ratios used to adjust column values for asymmetry.

Phylogeny, Body Mass, and Genetic Consequences of Lek-Mating Behavior in Hummingbirds

Robert Bleiweiss

Department of Zoology and the Zoological Museum, University of Wisconsin, Madison

The overt mate competition manifested in lek-type mating systems is thought to impart strong historical constraints on the origin and loss of lek behavior as well as to accelerate genetic evolution in lekking taxa. A DNA hybridization-based phylogeny for 26 hummminghirds (Trochilidae) was used to test these expectations through ancestral character state reconstruction and relative-rate tests (based on the index ΔT_mH-C) using an outgroup swift (Apodidae). Lekking developed at least eight times across the hummingbird lineages represented in the phylogeny, suggesting that lek behavior in these birds is not subject to strong historical constraints. Moreover, rate patterns differed from expectations for faster rates among lekkers in that: (1) the 2 lekking hermits (suhfamily Phaethornithinae) were evolving significantly more slowly than all 24 (lekking and nonlekking) nonhermits (subfamily Trochilinae); (2) analysis of covariance on the more numerous nonhermits alone or on the entire sample of species from both subfamilies indicated a significant negative effect of body mass (as covariate), but no significant effect of breeding system (as main effect), on rates of molecular evolution. Thus, molecular rate variation within and among breeding systems reflects both clade-specific effects on mean rates and a superimposed covariance between rates and body mass such that rates may be faster or slower depending on whether relatively smaller or larger size is favored. It is predicted that the frequent association of larger size with intense mate competition in many organisms may more often decrease the rate of molecular evolution under sexual selection, at least at the entire single-copy genome level measured by DNA hybridization.

Introduction

Leks, communal display grounds where males gather for the sole purpose of competing for mates, constitute one of the most remarkable forms of mating behavior expressed in animals. Although the striking social behaviors observed on leks have been subject to intensive study (Bradbury 1981; Höglund and Alatalo 1995), little is known about the genetic consequences of lekking. It is widely agreed that leks provide exceptional opportunities for the operation of sexual selection, both because individual behaviors at the lek suggest the operation of strong mate competition through female choice and male–male competition and because male reproductive success typically appears skewed such that one or a few individuals obtain most copulations. On this basis, various empirical and theoretical studies have suggested that leks may impart characteristic phylogenetic and population-genetic signatures. In particular, evidence that the behavior tends to cluster among related species in some groups has led to the claim that lekking has a strong historical component and evolves through selection on genetic variation for behavior (Prum 1994) rather than as a response to ecological conditions and social selection pressures (Emlen and Oring 1977; Foster 1985; Davies 1992). In addition, the intense sexual competition documented in lek-type mating systems is thought to accelerate evolution directly or indirectly by lowering effective population size, limiting gene flow between the traditional display arenas where males gather, and/or accelerating speciation through sexual isolation (Lande 1981; Kirkpatrick 1982; Arnold 1983; Bradbury and Gibson 1983; West-Eberhardt 1983). However, empirical estimates of rates of genetic change are missing from most discussions of the evolutionary dynamics associated with lekking behavior.

Two important considerations for studies of genetic evolution in relation to breeding system appear central to testing these generalizations further. The more obvious one is that a well-supported phylogenetic hypothesis must be available to examine the historical occurrence of lekking. The other factor is recent evidence that body mass often correlates inversely with rates of molecular evolution. Interest in this latter association has focused mainly on possible mechanisms mediating the link between greater body mass and slower rates of molecular evolution, especially on the roles of thermal habit and generation time (Martin and Palumbi 1993; Rand 1994; Mindell et al. 1996). However, the association between body mass and rate of molecular evolution has important implications for any process models that attempt to explain the evolution of body mass. Given that body mass is thought to be subject to sexual selection in a wide range of animals (Andersson 1994), predictions about molecular evolutionary rates associated with different breeding systems seem to require attention to body mass patterns.

Hummingbirds (Aves: Trochilidae) provide a useful group for examining the interrelationships of breeding systems and rates of molecular evolution for several reasons. Lek-mating behavior has been documented in numerous species in this diverse family (Snow 1974; Stiles and Wolf 1979; Payne 1984; Atwood, Fitz, and Bamesberger 1990; Bleiweiss 1997), being widespread in the depauperate subfamily of hermits (Phaethornithinae) but also occurring among many members of the diverse subfamily of nonhermits (Trochilinae). Moreover, hummingbird species differ by an order of magnitude in body mass, which in turn demonstrates a negative as-

Key words: body mass, DNA hybridization, hummingbirds, lek, phylogenetic constraint, relative rate.

Address for correspondence and reprints: Robert Bleiweiss, Department of Zoology and the Zoological Museum, University of Wisconsin, Madison, Wisconsin 53706. E-mail: reb@ravel.zoology.wisc.edu.

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sociation with relative rate of molecular evolution as measured by DNA hybridization distances (Bleiweiss 1998*a*). Despite these advantages, most previous analyses of lek evolution have excluded hummingbirds, because no reliable phylogeny was available for the family (Höglund 1989; Oakes 1992; but see Bleiweiss 1997). Here, I use a recently published DNA hybridization-based phylogeny for 26 species comprising the principal hummingbird lineages (Bleiweiss, Kirsch, and Matheus 1997) to examine the association of breeding systems with phylogenetic relationship and with rates of single-copy DNA evolution, including consideration of the interrelationships among breeding system, rate of molecular evolution, and body mass. I report that lek-mating in hummingbirds lacks a strong phylogenetic component and a characteristic rate of molecular evolution. However, the persistent association between body mass and rates of molecular evolution leads to some counterintuitive predictions about the associations between breeding systems and rates of molecular change.

Materials and Methods

Independent Variables

The breeding systems of the hummingbirds as lek or nonlek types were determined from literature sources (compilation in Bleiweiss 1997) supplemented with personal field observations made in Ecuador. As far as is known, hummingbirds are polygynous and have female-only parental care (Johnsgard 1983). Lekking represents an extreme form of polygyny and is traditionally defined to include systems in which males congregate on display arenas that females visit for the sole purpose of mating, i.e., males are clustered in dense or loose aggregations and provide no resource to females other than sperm (Andersson 1994; Höglund and Alatalo 1995). As the breeding systems are not known for all species used in the phylogeny, I also classified species based on whether or not any congeneric form was known to lek, conducting analyses on taxa scored for breeding system at the species and genus levels. In addition to allowing for assessment of the effects of sample size on observed patterns, the scoring of breeding systems at the genus level has biological justification, because evolutionary rates of nonlekking species are potentially correlated with rates along paths of shared ancestry with related lekking species (Felsenstein 1985).

To ensure that body masses were accurate predictors of estimated genetic distances, I obtained body mass data on wild-caught birds from the source populations used in the phylogenetic studies, including the individuals that provided the DNA for hybridization experiments (locality data presented in Bleiweiss, Kirsch, and Matheus 1997; details on weighing methods provided in Bleiweiss 1998*a*). I lacked measures of body mass for the females of two species (*Heliothryx barroti* and *Eugenes fulgens*), but male, female, and average body masses for each species are highly correlated and give similar results (unpublished data). I therefore report analyses on male body mass.

Topology Estimation, Character Evolution, and Relative Rates

Experimental generation and analysis of the complete distance matrix used to estimate the phylogeny have been described in detail elsewhere, including steps taken to provide the most accurate estimates of genetic distance (ΔT_mH-C; Bleiweiss, Kirsch, and Matheus 1997). The most parsimonious reconstruction of breeding system evolution was assessed by implementation of the ancestral character state reconstruction algorithm available in MacClade (Maddison and Maddison 1992). Relative-rate tests (Sarich and Wilson 1967) were used to obtain estimates of molecular evolutionary rates among the hummingbird taxa. In such a test, one measures the distance (fitted path lengths on the bootstrap consensus topology) from a suitable outgroup to different members of a monophyletic ingroup with which the outgroup shares a common ancestor. Because all paths from the outgroup to the different ingroup members pass through the same root node, differences in the distances to the various ingroup taxa should reflect differences in evolutionary rates among ingroups, provided that these distances are accurate estimates of that change. The phylogeny identifies hermits and nonhermits as basal sister groups among extant hummingbirds and resolves several principal lineages among the nonhermits (Bleiweiss, Kirsch, and Matheus 1997). Previous examinations of these data indicate that outgroup specification does not alter correlations between relative-rate distances and predictor variables except for more terminal outgroups that limit ingroup sampling (Bleiweiss 1998*a*). To capture the broadest ranges of rate variation and of lekking taxa, the swift was used to estimate relative rates, thereby incorporating both hermit and nonhermit taxa in the comparisons.

Statistical Tests

Some of the variables examined here are correlated among themselves or with other confounding factors. Thus, not only body masses, but also elevational occurrences of species are negatively correlated with relative-rate distance such that high-elevation species are evolving more slowly (Bleiweiss 1998*b*). Although one might expect body mass to increase with elevation, the relationship is not statistically significant for this (Bleiweiss 1998*b*) or larger samples (Feinsinger et al. 1979) of hummingbirds. However, for the purpose of ensuring maximal independence of these variables, I regressed male body mass against the midpoint (see Bleiweiss 1998*a*) of each species' elevational occurrence to remove effects of elevation. General linear models were then used to examine the relationships of breeding system and residuals of male body mass to relative rates of molecular evolution. All variables were $\log_e$-transformed to improve distributional assumptions of parametric statistics. All statistical analyses were conducted in SAS for UNIX on a SPARCstation 20.

Results

Ancestral character state reconstructions indicate that lekking has developed numerous times among hum-

FIG. 1.—Occurrence of lekking and nonlekking species and genera over the hummingbird phylogeny based on symmetrized ΔT_mH-C values, as described in the text. Qualitatively similar results obtain for the topology based on unsymmetrized data (Bleiweiss, Kirsch, and Matheus 1997). Ancestral states were reconstructed in MacClade (Maddison and Maddison 1992), with lekking and nonlekking being coded as alternate unordered character states (species with variable expression of lekking behavior were coded as lekkers). Codes for references on breeding system: a = Johnsgard (1983); b = Hilty and Brown (1986); c = Gerwin and Zink (1989); d = Stiles and Skutch (1989); e = Fjeldså and Krabbe (1990); f = Tyrell and Tyrell (1990); g = personal observations. *Threnetes ruckeri* (b); *Eutoxeres aquila* (b); *Eulampis holosericeus* (f); *Androdon aequatorialis* (b); *Heliothryx barroti* (b, d); *Colibri coruscans* (b); *Doryfera ludovicae* (d); *Eriocnemis luciani* (g); *Heliodoxa jacula* (e); *Coeligena wilsoni* (g); *Coeligena torquata* (g); *Popelairia conversii* (d); *Oreotrochilus chimborazo* (e); *Lesbia victoriae* (b); *Aglaiocercus coelestis* (b); *Chlorostilbon mellisugus* (b); *Campylopterus villaviscencio* (d); *Orthorhyncus cristatus* (f); *Thalurania colombica* (b, d); *Amazilia tzacatl* (b, d); *Lampornis clemenciae* (a); *Eugenes fulgens* (a); *Archilochus colubris* (a); *Myrtis fanny* (e, g); *Philodice mitchellii* (d); *Acestrura mulsant* (b).

mingbirds, whether the occurrence of lekking is scored at the species or genus level (fig. 1). Other than the two hermit species, *Eutoxeres aquila* and *Threnetes ruckeri*, the nearest relatives of all other lekkers are nonlekking taxa (fig. 1). Overall, ancestral character state reconstruction suggests that lekking behavior developed no less than four (species) or eight (genus) times among the taxa in the phylogeny.

Plots of relative-rate estimates (ΔT_mH-C, from the outgroup swift) versus male body mass for the two categories of breeding systems reveal for each breeding system category the general negative association between body mass and relative rate evident in the data as a whole (fig. 2). Classification of taxa into the two breeding system categories adds two patterns to this overall trend. First, both male body mass and rates vary widely within breeding system categories scored at the species or genus level. Second, the two hermits are evolving significantly more slowly than all (lekking and nonlekking) nonhermits (Bleiweiss 1998*b*) despite being lekkers (figs. 1 and 2).

Although no statistically based comparative methods are available to take phylogenetic relationship into account when analyzing relative-rate data (Harvey and Pagel 1991; Bleiweiss 1998*a*), lack of a strong historical component to breeding behavior among species in the phylogeny reduces the problems of nonindependence among taxa as regards hypothesis testing with standard statistical tables. Among nonhermits or the entire sample, homogeneity of slope tests indicated nonsignificant interactions between male body mass and breeding system (table 1). Thus, the relationships between rate variation and male body mass appear to be similar for lekking and nonlekking birds. Subsequent analyses without the interaction term (ANCOVA; table 2) indicate no significant contribution of breeding system to rates of molecular evolution. Again, these results are similar regardless of the inclusiveness of the analyses (with respect to hermits) and of the taxonomic level at which breeding system was scored (species or genus). The sampling of hermit taxa was too sparse to allow for inclusion of subfamily (hermit or nonhermit) as a categorical factor in the above model. However, the same decrease in rate with an increase in male body mass is apparent between the two hermits (fig. 2). Indeed, the hermit *E. aquila* is among the largest hummingbirds (approximately 11.0 g; fig. 2) and is the slowest-evolving species in my sample even though it leks.

Discussion

Phylogenetic Signature of Lek-Mating Behavior

The repeated evolution of lek-mating behavior among hummingbirds is mirrored by the general plasticity of mating behavior in these birds, as several species are themselves known to lek in some years or regions but not others (Stiles and Wolf 1979). This phylogenetic and population-level lability of breeding behavior in hummingbirds contrasts with previous assertions for other birds that lek-mating behavior is phylo-

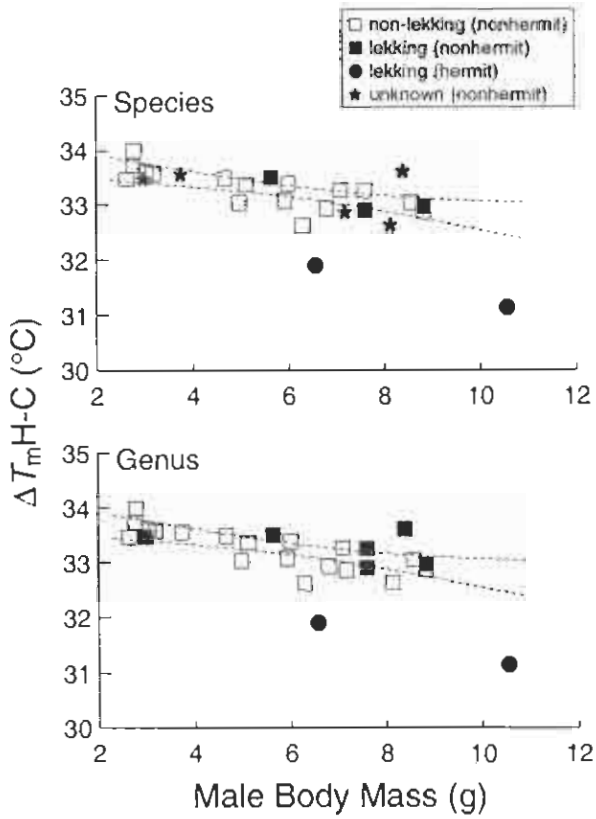

FIG. 2.—Scatter plots of raw values of relative rate (from outgroup swift (*Chaetura pelagica*) to ingroup hummingbirds) on raw male body mass. Average path lengths from *C. pelagica* based on unweighted least-squares tree-fitting ($P = 0$ in PHYLIP; Felsenstein 1993). See text for definitions of breeding systems and scoring of taxonomic categories. Dashed lines indicate 95% confidence interval for regression on nonhermits.

genetically conservative (Prum 1994). In particular, Prum (1994) suggested that lekking among manakins (Piprinae, Passeriformes) is under strong phylogenetic constraints, in that most members of this species-rich subfamily apparently retained lek-type breeding systems from their common ancestor. Possibly, the dynamics of lek-mating behavior in hummingbirds differ from those in other lekking birds in some fundamental way. However, Prum defined lekking to include species demonstrating either aggregated (many manakins) or solitary (e.g., *Heterocercus* manakins) display, whereas the traditional definition of a lek specifies male aggregation as well as lack of male provisioning of resources to females (Höglund and Alatalo 1995). Consequently, the only nonlekking manakin identified by Prum was *Antilophea galeata*, a derived taxon whose females nest inside male territories (Marini and Cavalcanti 1993). Even under Prum's more liberal definition, lekking was apparently lost in striped manakin (*Machaeropterus regulus*) populations in southeastern Brazil, where males are solitary and call from small fruiting trees (Melastomataceae) that provide a food source for visiting females (Sick 1993; unpublished data). Coincidentally, physiographic and biotic conditions in southeastern Brazil are distinctly different from those prevailing elsewhere in the humid lowlands of South America (Sick 1993), suggesting that the shift in Brazilian *Machaeropterus*' breeding system has an ecological cause, as does the shift in *Antilophea* (Marini and Cavalcanti 1993; Prum 1994). Based on a traditional characterization of lekking, up to five losses (*Antilophea, Heterocercus, Machaeropterus*, two taxa with unknown breeding systems) of lek-mating in manakins are possible in the context of Prum's (1994) phylogenetic hypothesis.

In light of the apparent ecological basis for shifts in mating behavior in some lekking birds (Snow 1973; Marini and Cavalcanti 1993; Prum 1994), it is reasonable to suggest that the lability of this breeding behavior in any particular taxon may relate more to that group's ecological plasticity; for example, the evolutionary lability of lek-mating behavior in hummingbirds (Stiles and Wolf 1979) is associated with a corresponding plasticity in ecological behaviors associated with exploitation of nectar, which is central to other hummingbird behaviors (Stiles 1981).

Relative Rates of Single-Copy DNA Evolution

Previous analyses of these DNA hybridization data suggested that outgroup-to-ingroup path length differences were unlikely to be caused by either base-compositional biases or differences in genome structure (Bleiweiss 1998*a*, 1998*b*). Moreover, experimental error did not affect correlations between path lengths and various independent variables when relatively distant taxa such as the swift or basal hummingbirds were used as the outgroups for estimating relative rates (Bleiweiss 1998*a*). Thus, despite a relatively small sample of taxa, the present analyses can be interpreted as providing ev-

Table 1
General Linear Model for ΔT_mH-C as Independent Variable[a] with Breeding System (BREED) as Main Effect and Male Body Mass (MASS) as Covariate

Source	df	Type III Sum of Squares	Mean Square	*F* Value	$P > F$
Species					
Hermits plus nonhermits					
BREED[b]	1	0.000396	0.000396	2.69	0.1193
MASS[c]	1	0.000980	0.000980	6.66	0.0194
BREED × MASS	1	0.001118	0.001118	7.59	0.0135[d]
Error	17	0.002502	0.000147		
Corrected total	20	0.007254			
Nonhermits					
BREED	1	0.000124	0.000124	1.70	0.2125
MASS	1	0.000980	0.000980	13.41	0.0023
BREED × MASS	1	0.000035	0.000035	0.48	0.4998
Error	15	0.001096	0.000073		
Corrected total	18	0.002236			
Genus					
Hermits plus nonhermits					
BREED	1	0.000006	0.000006	0.03	0.8708
MASS	1	0.001082	0.001082	5.15	0.0333
BREED × MASS	1	0.000146	0.000146	0.70	0.4132
Error	22	0.004621	0.000210		
Corrected total	25	0.007969			
Nonhermits					
BREED	1	0.000088	0.000088	1.10	0.3069
MASS	1	0.001082	0.001082	13.48	0.0015
BREED × MASS	1	0.000067	0.000067	0.84	0.3708
Error	20	0.001606	0.000080		
Corrected total	23	0.002805			

[a] Relative-rate distances based on unweighted least-squares ($P = 0$ in PHYLIP 3.5; Felsenstein 1993).
[b] Breeding system: lekking or nonlekking.
[c] Log, residual male body mass regressed on midpoint of elevational occurrence.
[d] Not significant after Bonferroni correction for four simultaneous comparisons.

idence for hummingbirds that no simple correlation exists between lek-breeding and rates of single-copy DNA evolution as measured by DNA hybridization data. In particular, the two lekking hermits examined here are evolving much more slowly than either nonlekking or lekking members of the nonhermit subfamily. Moreover, rates of single-copy DNA evolution within either hermits or nonhermits appear to depend strongly on body mass, which varies widely among members of either breeding system such that lekking is not associated with a characteristic overall rate in hummingbirds.

It could be argued a priori that there is no expectation for estimates of rates derived from the entire single-copy genome indexed by DNA hybridization to be coupled with genetic loci for traits, which might in this case be targets of selection. Nevertheless, given a connection between body mass and overall rate of molecular evolution (Martin and Palumbi 1993; Rand 1994), any selective force that acts on body mass thereby acts on molecular evolution, if only indirectly. Moreover, as body mass typically has a polygenic basis (Falconer 1973), a whole-genome approach to genetic correlates of body mass is biologically sensible. The association of body mass with evolutionary rate could be the indirect consequence of an association of body mass with some uncontrolled variable that affects the rate of molecular evolution. Body mass and generation time are positively associated in many groups of organisms, and rates of molecular evolution often are associated with both factors (Martin and Palumbi 1993). As many lekking species delay sexual maturation for several years (Andersson 1994), one might even expect slow rates of molecular evolution in lekkers (e.g., hermits) through the negative association of generation time and rates (Martin and Palumbi 1993; Mooers and Harvey 1994; Rand 1994). In other studies of the same hummingbird species, however, generation times appeared to be uncorrelated with rates (Bleiweiss 1998*a*).

One mechanism providing a direct connection between body mass and evolutionary rate within breeding systems is natural selection, which in hummingbirds may link body mass to foraging behaviors compatible with lek-mating behaviors (Stiles and Wolf 1979; Stiles 1981). In particular, both large and small sizes (masses) may be associated with feeding strategies that lead to an abandonment of resource-centered mating systems in favor of lekking ones (Stiles and Wolf 1979). These strategies include marauding by large-bodied species that have preferred access to the richest nectar sources, as well as nonterritoriality by small-bodied species that cannot displace territorial species (Feinsinger and Colwell 1978; Stiles and Wolf 1979). Alternatively, differences in body mass may reflect corresponding differences in sexual display. Small-bodied hummingbirds often have dynamic aerial sexual displays and may have become small through selection for greater maneuvera-

Table 2
ANCOVA for ΔT_mH-C as Independent Variable[a] with Breeding System (BREED) as Main Effect and Male Body Mass (MASS) as Covariate

Source	df	Type III Sum of Squares	Mean Square	*F* Value	$P > F$
Species					
Hermits plus nonhermits					
BREED[b]	1	0.000140	0.000140	0.69	0.4154
MASS[c]	1	0.001834	0.001834	9.12	0.0074
Error	18	0.003623	0.000201		
Corrected total	20	0.007254			
Nonhermits					
BREED	1	0.000126	0.000126	1.78	0.2006
MASS	1	0.001096	0.001096	15.50	0.0012[d]
Error	16	0.001131	0.000071		
Corrected total	18	0.002236			
Genus					
Hermits plus nonhermits					
BREED	1	0.000003	0.000003	0.01	0.9062
MASS	1	0.002334	0.002334	11.26	0.0027
Error	23	0.004767	0.000207		
Corrected total	25	0.007969			
Nonhermits					
BREED	1	0.000147	0.000147	1.85	0.1884
MASS	1	0.001129	0.001129	14.17	0.0011
Error	21	0.001673	0.000080		
Corrected total	23	0.002805			

[a] Relative-rate distances based on unweighted least-squares ($P = 0$ in PHYLIP 3.5; Felsenstein 1993); interaction term for all comparisons nonsignificant and pooled with error.
[b] Breeding system: lekking or nonlekking.
[c] Log, residual male body mass regressed on midpoint of elevational occurrence.
[d] All covariates significant after Bonferroni correction for four simultaneous comparisons.

bility (Payne 1984). In contrast, large-bodied species tend to have rather static displays with fewer motion-oriented elements. Under either scenario, a wide range of body masses and, hence, rates of genetic evolution would be expected within breeding system categories.

Of course, given a similar distribution of body sizes, one may still ask why there is no additional effect of breeding system (the main effect in the ANCOVA) among species of similar masses. After all, the highly unusual dispersion and sexual behaviors of lekking birds leads to the expectation that this breeding system should promote a distinctive population structure and thus be associated with characteristic rates of evolution. However, the assumption that all lekking systems generate the same set of underlying evolutionary dynamics may be incorrect. Most obviously, species that lek in some regions or years but not in others (Stiles and Wolf 1979) could lack a distinct genetic signature as a consequence of their variable mating behaviors. Collectively, moreover, species that express lek-mating behavior define a characteristic subset of plumage phenotypes, from dull monomorphic to bright dimorphic (Bleiweiss 1997), that could reflect corresponding differences in population parameters that affect genetic dynamics.

Conclusions

The results of this study suggest that lekking hummingbirds lack a characteristic genetic signature at two levels. First, the repeated evolution of lekking behavior argues against strong phylogenetic components to the development of lekking. Second, lekking does not appear to be associated with a characteristic, or necessarily faster, rate of change at the whole-genome level. Indeed, lekking even may be associated with relatively slow rates, as exemplified by the slower clade-specific rate of hermits. This departure of hermits from rates observed in other hummingbirds remains unexplained, and better data on generation time and other aspects of hermit biology that might account for this pattern are needed. An important caveat to the generality of the nonsignificant rate differences between lekkers and nonlekkers reported here is that as far as is known, hummingbirds express only polygynous mating systems (Johnsgard 1983). Future studies should compare polygynous and nonpolygynous (monogamous) taxa, which might differ sufficiently in population dynamics to produce characteristic rate differences.

This study also highlights the need to consider covariation with other variables when attempting to evaluate mean differences in focal attributes of lekking and nonlekking birds (see also Bleiweiss 1997). In this regard, the additional support hummingbirds lend to a general association between larger body mass and slower rates of molecular evolution leads to some important generalizations about patterns of genetic evolution in relation to breeding systems. In particular, the relationship between genomic evolution and sexual selection can be predicted for any group that demonstrates a significant (negative) association between body mass and rate of molecular evolution. As sexual selection favors large body mass in many groups (Höglund and Alatalo 1995), the process

may be associated more often with slower than with faster rates of overall single-copy DNA evolution.

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Relative-Rate Tests and Biological Causes of Molecular Evolution in Hummingbirds

Robert Bleiweiss

Department of Zoology and the Zoological Museum, University of Wisconsin, Madison

Hummingbirds (Trochilidae) present extreme variation in several factors thought to affect rates of molecular evolution, including generation time, species diversity, body mass, and metabolic rate. A published DNA hybridization phylogeny was used to examine experimental and biological causes of apparent rate variation among 26 species representing the principal lineages in the family. Molecular evolutionary rates (fitted path lengths based on ΔT_mH-C) among the various lineages differed significantly as determined by Felsenstein's F ratio test. Parametric and nonparametric correlations between relative rates and various predictor variables were qualitatively similar for outgroup species within and across different lineages except for outgroups that required comparisons among a small set of ingroups. Thus, the relative-rate tests appeared to be less sensitive to outgroup specification than to ingroup sampling. Correlations and analyses of covariance with predictor variables and outgroup species nested within the principal lineage indicated consistently significant associations of relative rates with various measures of body mass (negative) and with some mass-specific measures of basal metabolic rate (positive), but not with generation time or species diversity. These patterns held even if correlations among predictor variables were taken into account. Overall, these results for hummingbirds are consistent with hypotheses that relate metabolic processes associated with oxygen consumption to rates of molecular evolution. The results are incompatible with demographic (generation time, speciation) or body temperature effects on rates of DNA evolution. As DNA hybridization distances index the entire single-copy genome, the results also provide evidence for metabolic effects on evolutionary rates of the nuclear germ line.

Introduction

Hummingbirds (Trochilidae) provide a model system for investigating causes of variation in rates of molecular evolution, because they represent the vertebrate extreme for several demographic and physiologic factors with possible links to rate variation (Rand 1994). However, hummingbirds' suite of exceptional attributes also highlights some general problems in distinguishing among the various factors proposed to govern rates of molecular evolution. Based on their general characteristics, hummingbirds might be predicted to have a faster rate of molecular evolution than related birds (Rand 1994) because of their short generation times (Sibley and Ahlquist 1990), great species richness (Bleiweiss 1991), and high metabolic rates (Suarez et al. 1991). Indeed, some previous evidence based on DNA hybridization distance data suggests that hummingbirds are evolving faster than related nonpasserine birds (Bleiweiss, Kirsch, and Lapointe 1994). However, most of the factors enumerated above are correlated across higher taxonomic groups such that specific causes of the rate signature of a higher taxon are difficult to isolate (Hasegawa and Kishino 1989; Mooers and Harvey 1994; Mindell et al. 1996). Specifically, generation time and species diversity themselves may be correlated through the former's effect on rates of population divergence (Brown and Gibson 1983; Kochmer and Wagner 1988; Reaka-Kudla 1991), and generation time and species diversity may correlate with metabolic rate through the common factor of body mass (Bennett and Harvey 1987; Martin and Palumbi 1993; Mooers and Harvey 1994). Unfortunately, few studies of rate variation have successfully isolated these different effects, and the paucity of available data also makes difficult any quantification of experimental error, which may be a problem, especially for tests that rely on distance measures.

A particular advantage of hummingbirds as regards these confounding influences is that demographic and physiologic factors are not completely covariant within the family. Rather, many life history parameters appear to be constrained by the birds' adaptations to feeding at flowers, whereas the family's overall evolutionary radiation within the nectar-feeding niche has generated surprising physiologic and morphologic diversity. Thus, all hummingbirds appear to lay two eggs, have the same nectar-dependent diets, and breed within their first year of life (Bent 1940; Skutch 1972; Carpenter 1976; Brown, Calder, and Kodric-Brown 1978), whereas species differ by an order of magnitude in body mass (Carpenter 1976; Wolf and Gill 1986).

Here, I use a published DNA hybridization phylogeny for 26 hummingbird species (Bleiweiss, Kirsch, and Matheus 1997) to examine rate variation and its associations with various demographic (generation time, speciation as measured by taxonomic diversity), morphologic, and physiologic variables. Associations are examined through application of relative-rate tests (Sarich and Wilson 1967), which measure genetic distances from an outgroup to members of a monophyletic ingroup with which the outgroup shares a common ancestor; differences in genetic distance along these paths are taken to represent rate variation among ingroup lineages (fig. 1; Sarich and Wilson 1967; Easteal, Collet, and Betty 1995). Relative-rate tests are independent of fossil calibration dates and therefore can be applied to groups with a poor historical record such as is the case

Key words: body mass, DNA hybridization, generation time, hummingbirds, metabolic rate, relative-rate test.

Address for correspondence and reprints: Robert Bleiweiss, Department of Zoology and the Zoological Museum, University of Wisconsin, Madison, Wisconsin 53706. E-mail: reb@ravel.zoology.wisc.edu.

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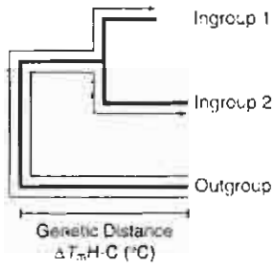

FIG. 1.—Distance-based relative-rate tests from an outgroup to two ingroup taxa. A slower rate is inferred for ingroup 1 based on a shorter path length from outgroup to ingroup 1 than to ingroup 2.

for hummingbirds (Olson and Hilgartner 1982; Bleiweiss 1998*a*), thus also avoiding errors in rate estimates introduced by uncertainties in the geologic record (Easteal, Collet, and Betty 1995; Springer 1995). However, relative-rate tests may fail to discern rate differences or may give spurious results depending on characteristics of the outgroup chosen to make such tests (Easteal, Collet, and Betty 1995; Springer 1995; Hillis, Mable, and Moritz 1996). As described below, the comprehensive phylogeny lends itself to a rigorous experimental design for isolating biological from various experimental causes of apparent rate variation.

Hummingbird Phylogeny and Design of Relative-Rate Tests

With respect to construction of relative-rate tests, the key well-corroborated features of hummingbird phylogeny (fig. 2) are their distant sister group relationship to swifts (Sibley and Ahlquist 1990; Bleiweiss, Kirsch, and Lapointe 1994); their own basal division into so-called hermit and nonhermit lineages (Bleiweiss, Kirsch, and Matheus 1997; formally recognized as the subfamilies Phaethornithinae and Trochilinae, respectively); and the subdivision of nonhermits into six principal lineages that contain the bulk (over 300 species) of hummingbird taxonomic and phenotypic diversity: mangoes, brilliants, coquettes, emeralds, mountain gems, and bees (fig. 2; for details see Bleiweiss, Kirsch, and Matheus 1997). Along with swifts and hermit hummingbirds, these principal lineages will be referred to as the "named clades" to distinguish them from their member species.

The one formal requirement for constructing relative-rate tests is that the paths from the outgroup must pass through an internal node shared by all ingroup taxa (fig. 1). In the context of the branching hierarchy of the named hummingbird clades, this constraint implies a natural hierarchy of rate comparisons; each successively more terminal named clade provides a set of outgroups for relative-rate measurements to a reduced subset of ingroups (table 1, fig. 2). This "subset" design facilitates examination of the possible effects of both outgroup mean distance (named clades) and experimental replication (species within named clades), which may impose one or more biases on correlations between relative-rate distances and biologically relevant variables. For instance, relative-rate differences are confined to the unshared portion of the path from outgroup to ingroup, which thereby comprises proportionately less of the total path measured from more distant outgroups. Added to such autocorrelation, more distant outgroups also may

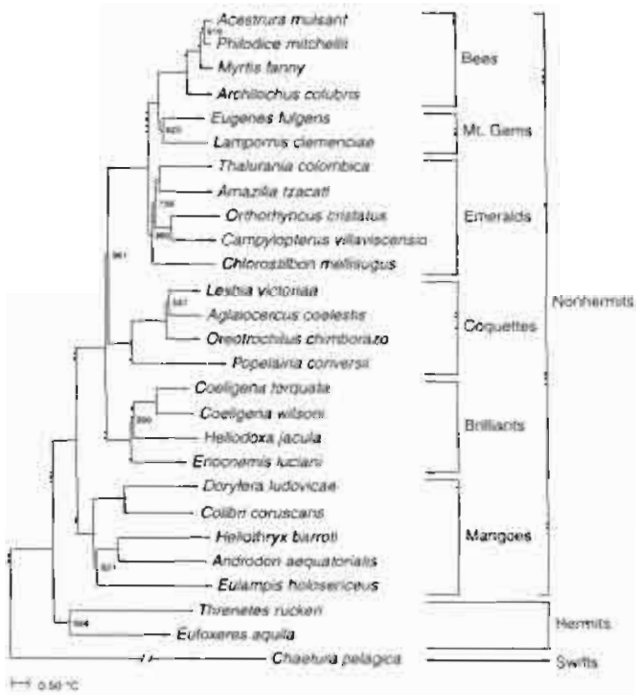

FIG. 2.—Consensus bootstrap FITCH topology based on symmetrized ΔT_mH-Cs (see text for additional details). Branch lengths are averages over the 1,000 bootstrap pseudoreplicate trees and are drawn to scale for hummingbirds. Numbers indicate trees supporting a node out of the 1,000 bootstrap pseudoreplicate trees (if less than 100%). Named clades are as defined in text.

Table 1
Design of Relative-Rate Tests

Outgroup	*N*	Ingroups	*N*
Swift	1	Hermits; mangoes; brilliants; coquettes; emeralds; mountain gems and bees	26
Hermits	2	Mangoes; brilliants; coquettes; emeralds; mountain gems and bees	24
Mangoes	5	Brilliants; coquettes; emeralds; mountain gems and bees	19
Brilliants	4	Coquettes; emeralds; mountain gems and bees	15
Coquettes	4	Emeralds; mountain gems and bees	11
Emeralds	5	Mountain gems and bees	6
Mountain gems and bees	6	Emeralds	5

NOTE: See figure 2 for topology and species membership in named clades. Emeralds or mountain gems and bees can be designated as the terminal clade of outgroups.

suffer greater saturation in nucleotide substitution rates caused by multiple hits and reversals in base substitutions (Jukes and Cantor 1969). On the other hand, more terminal outgroups serve to compare relatively fewer ingroups, which may contribute to sampling bias.

The several species within each named clade themselves provide replicate outgroups for an examination of variation (in correlations of relative-rate distances with biologically relevant variables) associated with each outgroup's DNA, which contributes one strand to all duplex DNAs made for that outgroup's set of comparisons (Sheldon and Bledsoe 1989; Bleiweiss and Kirsch 1993*a*, 1993*b*). The experimental errors contributed by the outgroup DNA arise from many sources, but principally from the DNA extraction and radioactive-labeling procedures, of which the latter is associated with a markedly high variance in melting temperature (Bleiweiss and Kirsch 1993*b*). Inconsistent associations between predictor variables and relative-rate measures from different outgroups within named clades would suggest that relative-rate measures simply are not sufficiently accurate or precise for testing hypotheses about evolutionary rates, regardless of any biases evident at the higher level of the named clades.

Materials and Methods

Hypotheses of Rate-Variation and Predictor Variables

Generation Time

The original suggestion of Laird, McConaughty, and McCarthy (1969) was that rate variation depends inversely on generation time or its various correlates, including the number of germ line replications per year (Britten 1986; Li, Tanimura, and Sharp 1987) and age at first breeding (Sibley and Ahlquist 1990). Although available evidence indicates that all hummingbirds breed before the end of their first year of life (Bent 1940; Johnsgard 1983), interspecific variation in age at first breeding appears to occur within this narrow time frame. At one extreme, some hummingbirds are seasonal breeders that emigrate from their breeding grounds until the following year. These species include temperate high-latitude forms that are long-distance migrants and many tropical montane species that are elevational migrants. At the other extreme, resident tropical (mostly lowland) species potentially breed at any time of year (continuously), thereby allowing for the possibility that their generation times are different (shorter) than those of migratory species. For example, immature male hermits (*Phaethornis superciliosus*) begin to attend lek display areas within 3–4 months of fledging, with peak recruitment by 6–8 months (Stiles and Wolf 1979). Finally, idiosyncratic patterns occur in species such as the Andean hillstar (*Oreotrochilus estella*), which lives in a very seasonal high-altitude environment (Carpenter 1976). Immature hillstars acquire adult plumage and potential breeding status prior to their first winter, within 7 months of fledging (Carpenter 1976). Thus, even though most hummingbirds appear to mate in their first year of life, important differences in breeding patterns among species may impart different generation times.

I quantified these breeding patterns in three ways. First, a continuous measure of differences in breeding patterns is provided by the duration of the breeding season (in months, estimated from literature records of the earliest and latest dates on which active nests were found for a particular species). Generation time may associate negatively with duration of breeding season, in that longer breeding seasons allow for earlier ages at first reproduction, whereas shorter breeding seasons constrain some or all first-year birds to wait until the next annual cycle to breed. Under the generation-time hypothesis, therefore, rates of molecular evolution may associate positively with duration of breeding season. I also assigned integer rankings of generation time (from long to short) based on periodicity of breeding seasonality (seasonal, accelerated [e.g., *Oreotrochilus*], or continuous breeders) or based on migratory habits (long-distance migrant, pronounced elevational migrant, elevational migrant, resident). These categories also may reflect constraints that set different lower limits on the interval between breeding seasons and thus may correlate with generation time.

Species Diversity

Analogous to generation time, it has also been suggested that rates of genetic change are directly proportional to rates of species formation and the demographic consequences associated with cladogenesis (Avise and Ayala 1976; Avise and Aquadro 1982; Mindell, Sites, and Grauer 1989; Barraclough, Harvey, and Nee 1996). As the phylogeny encompasses less than 10% of all hummingbird species, rates of cladogenesis were estimated indirectly as the number of congeneric species per terminal taxon (numbers obtained from standard literature sources [Peters 1945; Monroe and Sibley 1993]). Given that relative-rate tests discriminate rate-variation toward the tips of the phylogeny, some measure of cladogenesis near the tips is biologically reasonable.

Physiology

The two physiologic mechanisms proposed to govern molecular rate variation make contrasting predictions about both the underlying cause of rate variation and its correlation with proxy variables such as body mass. The body temperature hypothesis proposes that elevated body temperatures limit the number of functional variants of a protein, thereby constraining the number of substitutions permissible in regions of DNA that code for that protein (Prager et al. 1974; Somero 1978; Mindell et al. 1996). Consequently, the hypothesis predicts that the rate of molecular evolution will increase with body mass and the corresponding decrease in mean body temperature. The alternative metabolic-rate hypothesis is based on the observation that rates in some groups decrease with body mass, leading to the explanation that physiological processing of oxygen increases free radical production and/or rates of DNA synthesis and, hence, nucleotide replacement rates in smaller-bodied forms (Kocher et al. 1989; Thomas and Beckenback 1989; Martin, Naylor, and Palumbi 1992; Ada-

chi, Cao, and Hasegawa 1993; Martin and Palumbi 1993).

Literature values of basal metabolic rate (BMR) measured in kilocalories per day were available for eight taxa (Bennett and Harvey 1987) represented in the DNA hybridization study. Although Bennett and Harvey report several different values of BMR for some of these species, I used those values selected for analysis by Bennett and Harvey (1987); they chose the lowest reported value under the supposition that BMR represents a minimum value within the zone of thermoneutrality. Given that BMR and body temperature are highly correlated with body mass among homeotherms (Schmidt-Nielsen 1984), I used body mass both as another predictor variable and as a proxy measure of both metabolic rate and body temperature. To ensure that genetic data were matched to accurate measures of body mass, I obtained mass data on wild-caught birds from the source populations used in the DNA hybridization experiments (locality data presented in Bleiweiss, Kirsch, and Matheus 1997). Birds were weighed with a Pesola scale to the nearest 0.1 g (> 5.0 g) or 0.05 g (<5.0 g) immediately after capture by placing them in preweighed cloth bags. As hummingbirds show significant sexual size dimorphism (Payne 1984), I estimated the mean for each sex as well as a species mean defined as the midpoint between the two sex-specific means; females of *Heliothryx barroti* and *Eugenes fulgens* were not captured, so their values cannot be reported. For similar reasons, mass-specific BMRs were calculated based on the values given for body mass in conjunction with BMR data (in Bennett and Harvey 1987).

Estimation of Genetic Distances

Experimental and Analytical Methods

Procedures for generation of the complete matrix of reciprocal distances are detailed elsewhere (Bleiweiss, Kirsch, and Matheus 1997). Briefly, a series of experimental and algorithmic methods were used to improve the accuracy of measured distances and fitted path lengths, including use of median melting temperature (T_m) to index genetic change across more of the genome; use of different individuals to generate each replicate measure to provide the best assessments of both average distance and replicate variance for bootstrap resampling; corrections for normalized percentage of hybridization (NPH) and homoplasy (Jukes and Cantor 1969) to yield the index T_mH-C (transformation equations and justifications given in Bleiweiss, Kirsch, and Matheus 1997). The complete distance matrix was then constructed by converting the raw distances to delta values (ΔT_mH-C), calculated as the difference from the homologous (the radioactively labeled strand matched to a second strand from the same species) to the heterologous (the labeled strand matched to a different species) hybrids. For the detection of rate differences among taxa, symmetrization of the distance matrix is important, because it eliminates systematic experimental error that could be mistaken for rate variation, such as through compression of distances caused by lower melting temperatures among the homologous standards used to estimate delta values (Springer and Kirsch 1991).

Rate Variation

Test of Significant Rate Variation

I tested for overall deviations from uniform rates of molecular evolution among lineages (molecular clock) through application of Felsenstein's (1993) F ratio test, for which ΔT_mH-C provides the most appropriate index (Springer and Kirsch 1989). This test evaluates whether the sum of squares (SS) of the tree-fitted distances of the best-fit FITCH tree (no assumption of clock) is significantly smaller than the sum of squares of the tree-fitted distances obtained for the best-fit KITSCH tree (assumption of clock), as given by:

$$(SS_{KITSCH} - SS_{FITCH}/df_{KITSCH} - df_{FITCH}) \div (SS_{FITCH}/df_{FITCH}),$$

here using the more conservative assignment of degrees of freedom (no accounting of the number of subreplicates; Felsenstein 1993), in which case $df_{KITSCH} = [(n^2 - n)/2] - (n - 1)$, $df_{FITCH} = [(n^2 - n)/2] - (2n - 3)$, and n is equal to the number of taxa (27). The average bootstrapped (1,000 times) path lengths from the designated outgroup to all appropriate ingroup taxa (Bleiweiss, Kirsch, and Matheus 1997) then served to estimate relative rates for testing associations between rates and the predictor variables (table 2 and fig. 2).

Tests of Significant Associations

I $\log_e$-transformed both dependent and predictor variables to improve normality and/or homogeneity of variance. Male body mass was used to remove mass-dependent effects from other variables (duration of breeding season, species diversity, metabolic rate), because I lacked measures of female body mass for two species. As body mass itself may be associated with environmental variables such as elevation (Mayr 1963), I removed the potential confounding effects of the latter on mass by regressing body mass on the midpoint between the minimum and maximum elevational occurrence of each species. Other measures of elevational occurrence (minimum or maximum) gave qualitatively similar results. Residual analyses excluded the swift, which was used only as an outgroup.

Statistically based comparative methods to account for nonindependence caused by phylogenetic relatedness are not developed for relative-rate data, as comparative methods also use branch lengths to standardize contrasts so that the usual probability tables can be employed for testing hypotheses (Harvey and Pagel 1991; Garland, Harvey, and Ives 1992). Therefore, I designed statistical analyses of associations between path lengths and the various predictor variables to facilitate comparisons with previous studies of relative-rate variation, in particular, those based on DNA hybridization data (Mooers and Harvey 1994). To assess the effects of outgroup specification, I examined patterns in the occurrence of significant correlations (both parametric and nonparametric) in a matrix of all such comparisons between the 27 outgroups and 15 predictor variables (including raw val-

Table 2
Average Path Length Half-Matrix for Symmetrized ΔT_mH-C Among the 26 Hummingbirds and Swift (*Chaetura pelagica*) Used for Relative-Rate Tests

	LC	*TC*	*AC*	*CW*	*EL*	*EH*	*CC*	*EF*	*AM*	*AO*	*MF*	*PM*	*AT*	*CV*	*AA*	*LV*	*DL*	*OC*	*HJ*	*HB*	*CM*	*CT*	*PC*	*OS*	*TR*	*EA*	*CP*
LC	0.00																										
TC	4.12	0.00																									
AC	6.40	6.55	0.00																								
CW	6.34	6.48	6.08	0.00																							
EL	6.10	6.24	5.84	4.03	0.00																						
EH	8.98	9.13	8.72	8.51	8.27	0.00																					
CC	8.47	8.61	8.20	7.99	7.75	7.40	0.00																				
EF	2.92	4.04	6.33	6.26	6.02	8.91	8.39	0.00																			
AM	3.50	4.34	6.62	6.56	6.32	9.20	8.68	3.39	0.00																		
AQ	3.41	4.25	6.53	6.47	6.23	9.11	8.59	3.30	1.71	0.00																	
MF	3.51	4.34	6.63	6.56	6.32	9.20	8.69	3.39	0.88	1.72	0.00																
PM	3.42	4.26	6.54	6.47	6.23	9.12	8.60	3.31	0.54	1.63	0.81	0.00															
AT	4.13	3.56	6.56	6.49	6.25	9.13	8.62	4.05	4.35	4.26	4.35	4.26	0.00														
CV	4.25	4.02	6.68	6.62	6.37	9.26	8.74	4.18	4.47	4.38	4.47	4.39	4.03	0.00													
AA	8.80	8.95	8.54	8.33	8.08	7.61	7.21	8.72	9.02	8.93	9.02	8.94	8.95	9.08	0.00												
LV	6.36	6.50	2.12	6.03	5.79	8.67	8.16	6.28	6.58	6.49	6.58	6.50	6.51	6.64	8.49	0.00											
DL	8.53	8.67	8.26	8.05	7.81	7.46	4.81	8.45	8.75	8.66	8.75	8.66	8.68	8.81	7.28	8.22	0.00										
OC	6.37	6.52	2.22	6.04	5.80	8.68	8.17	6.30	6.59	6.50	6.59	6.51	6.52	6.65	8.50	2.12	8.23	0.00									
HJ	6.45	6.59	6.19	4.15	4.14	8.62	8.10	6.37	6.67	6.58	6.67	6.59	6.60	6.73	8.44	6.14	8.17	6.16	0.00								
HB	8.96	9.10	8.69	8.48	8.24	7.77	7.37	8.88	9.17	9.08	9.18	9.09	9.11	9.23	6.09	8.65	7.43	8.66	8.59	0.00							
CM	4.24	4.12	6.67	6.61	6.37	9.25	8.73	4.16	4.46	4.37	4.46	4.37	4.13	4.23	9.07	6.63	8.80	6.64	6.72	9.23	0.00						
CT	6.11	6.25	5.85	2.41	3.79	8.28	7.76	6.03	6.33	6.24	6.33	6.24	6.26	6.38	8.09	5.80	7.82	5.81	3.92	8.25	6.38	0.00					
PC	7.31	7.45	5.50	6.98	6.74	9.62	9.11	7.23	7.53	7.44	7.53	7.45	7.46	7.59	9.44	5.46	9.17	5.47	7.09	9.60	7.58	6.75	0.00				
OS	4.37	4.14	6.80	6.73	6.49	9.38	8.86	4.30	4.59	4.50	4.59	4.51	4.15	3.12	9.20	6.76	8.92	6.77	6.85	9.35	4.35	6.50	7.71	0.00			
TR	10.70	10.84	10.43	10.22	9.98	10.75	10.23	10.62	10.92	10.83	10.92	10.84	10.85	10.98	10.57	10.39	10.30	10.40	10.34	10.72	10.97	9.99	11.34	11.10	0.00		
EA	9.96	10.10	9.69	9.48	9.24	10.01	9.49	9.88	10.18	10.09	10.18	10.10	10.11	10.24	9.83	9.65	9.56	9.66	9.60	9.98	10.23	9.25	10.60	10.36	7.52	0.00	
CP	33.34	33.48	33.07	32.86	32.62	33.38	32.87	33.26	33.55	33.46	33.56	33.47	33.49	33.61	33.20	33.03	32.93	33.04	32.97	33.36	33.60	32.63	33.98	33.73	31.90	31.15	0.00

NOTE.—Zeros along the diagonal indicate homologous comparisons ($\Delta = 0$). Species codes: *LC* = *Lampornis clemenciae*; *TC* = *Thalurania colombica*; *AC* = *Aglaiocercus coelestis*; *CW* = *Coeligena wilsoni*; *EL* = *Eriocnemis luciani*; *EH* = *Eulampis holosericeus*; *CC* = *Colibri coruscans*; *EF* = *Eugenes fulgens*; *AM* = *Acestrura mulsant*; *AO* = *Archilochus colubris*; *MF* = *Myrtis fanny*; *PM* = *Philodice mitchellii*; *AT* = *Amazilia tzacatl*; *CV* = *Camylopterus villaviscensio*; *AA* = *Androdon aequatorialis*; *LV* = *Lesbia victoriae*; *DL* = *Doryfera ludovicae*; *OC* = *Oreotrochilus chimborazo*; *HJ* = *Heliodoxa jacula*; *HB* = *Heliothrix barroti*; *CM* = *Chlorostilbon mellisugus*; *CT* = *Coeligena torquata*; *PC* = *Popelairia conversa*; *OS* = *Orthorhyncus cristatus*; *TR* = *Threnetes ruckeri*; *EA* = *Eutoxeres aquila*; *CP* = *Chaetura pelagica*.

Table 3
Predicted Correlations Between Predictor Variables and Rate of Molecular Evolution for Four Hypotheses

Hypothesis	Genetic Rate (dependent variable)	Body Mass (independent variable)
Generation time	Negative	Positive
Species diversity	Positive	Negative
Body temperature	Negative	Negative
Specific oxygen consumption	Positive	Negative

Table 4
***F* Ratio Test of Rate Variation Among Hummingbird Lineages**

Ingroups	n	SS_{KITSCH}	SS_{FITCH}	df_{KITSCH}	df_{FITCH}	F ratio	P
Hermits + nonhermits	27	571.696	268.403	325	300	13.56[a]	<0.001
Nonhermits	25	453.895	232.297	276	253	10.50[b]	<0.001

NOTE.—SS_{KITSCH} = sum of squares of the tree-fitted distances of the best-fit KITSCH tree; SS_{FITCH} = sum of squares of the tree-fitted distances of the best-fit FITCH tree.

[a] Degrees of freedom for *F*-test: 26, 300.

[b] Degrees of freedom for *F*-test: 24, 253.

ues and residuals). To assess overall significance of associations with relative rates (as dependent variable), I constructed separate general linear models analogous to analyses of covariance (ANCOVAs) in turn for each predictor variable (covariate), nesting the variable and outgroup species (main effect) under the corresponding named clades (blocks; mountain gems and bees treated as a single block). To maintain the "subset" design, one or the other terminal sister clade, emeralds or mountain gems and bees, was excluded in turn from the ANCOVA.

All analyses were based on path lengths from the consensus bootstrap FITCH topologies (fitted by unweighted least-squares, specifying $P = 0$ in FITCH; Felsenstein 1993). One-tailed critical values were used as the basis for testing the various hypotheses, which make specific directional predictions about the relationship between the independent and dependent variables (table 3). For the purpose of exploring data structure in the 27 × 15 table, I report nominal significance to $P < 0.10$. All statistical tests were performed in SAS for UNIX on a SPARCstation 20.

Results

Rate Variation

To implement the *F*-test, the topology generated by FITCH was forced for the KITSCH option by specifying a user-defined tree. The *F*-test indicates significant disparities in rates among hummingbird lineages as a whole and among just the more diverse nonhermits (table 4). As shown elsewhere (Bleiweiss 1998*b*), hermits are significant outliers for rate variation that exists among hummingbirds generally, and they were analyzed separately (as ingroups) from nonhermits.

Data Characteristics

The 24 ingroup species cover most of the intrafamilial variation observed for the 15 predictor variables (appendix) except that my sample omits the 20.0-g giant hummingbird *Patagona gigas* (a distinct outlier at the large end of hummingbird body masses; see Carpenter 1976). The distribution of significant correlations between path lengths and predictor variables in the 27 × 15 table of all such comparisons reveals several patterns (fig. 3). First, the overall significances of correlations between path lengths and predictor variables are remarkably similar for the suite of outgroup taxa within each named clade. Of the 86 such blocks of taxa in each table of correlations (excluding the singletons representing the swift clade and six blocks with insufficient observations to calculate a correlation), results are heterogenous within only three blocks for Pearson correlations (<3.5%) and within only two blocks for Spearman correlations (<2.4%). Of 172 such blocks across both tables, only one (<0.6%) has both significant and nonsignificant cell *P* values (by the criteria given above). This remarkable consistency suggests that the significance level of a correlation depends largely on characteristics common to members of the clade. Thus, differing results among named clades presumably result from analytical considerations and not from confounding experimental error such as might arise through factors that determine the melting temperature of a specific outgroup's DNA.

Consistent with this interpretation, the outgroup taxa within each named clade provide very similar path length statistics for the associated set of ingroup taxa, with characteristic levels of path length variation (standard deviation [fig. 4*a*] and standard error [fig. 4*b*]) associated with outgroups within each named clade. However, the statistics of variation in path lengths measured from outgroups at different depths in the tree indicate no simple trend (fig. 4), as might otherwise be expected from autocorrelation and/or saturation effects alone.

To quantify the tablewide occurrence of significant correlations, I scored each cell (in fig. 3) as a 1 (significant; one-tailed $P < 0.10$) or 0 (nonsignificant) and then applied tests of linear trends on these categorical scores across each group of predictor variables (demography [generation time, species diversity], body mass, metabolic rate). These tests indicate consistent results (nonsignificant for demographic variables, significant for body mass variables; table 5) for outgroups in more basal, but not more terminal, named clades. The overall inconsistent results that obtain for associations based on relative rates measured from more terminal outgroups (fig. 3) presumably are caused by sampling biases, and these patterns are difficult to interpret.

Effects of Predictor Variables on Rates of Molecular Evolution

For nonhermits, path lengths from most outgroups were significantly and negatively correlated with all measures of body mass. Significance levels for residuals (of mass regressed on elevational occurrence) some-

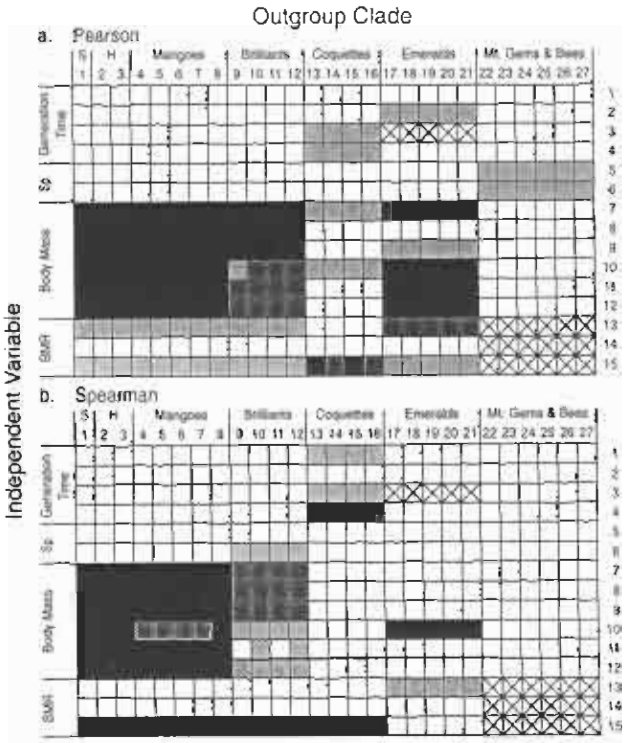

FIG. 3.—Schematic representation of results for Pearson (*a*) and Spearman (*b*) correlations (raw correlations, exact two-tailed *P* values, and sample sizes available from the author) with relative rates. Shading indicates level of significance: black for two-tailed significance at $P < 0.05$, dark gray for one-tailed significance at $P < 0.05$, light gray for one-tailed significance at $P < 0.10$, and white for nonsignificance (see text for further discussion). Hatched cells had too few observations for correlations to be calculated. Horizontal cells correspond to outgroup taxa grouped by outgroup (named) clade: 1 = *Chaetura pelagica*; 2 = *Threnetes ruckeri*; 3 = *Eutoxeres aquila*; 4 = *Eulampis holosericeus*; 5 = *Colibri coruscans*; 6 = *Androdon aequatorialis*; 7 = *Doryfera ludovicae*; 8 = *Heliothryx barroti*; 9 = *Coeligena wilsoni*; 10 = *Eriocnemis luciani*; 11 = *Heliodoxa jacula*; 12 = *Coeligena torquata*; 13 = *Aglaiocercus coelestis*; 14 = *Lesbia victoriae*; 15 = *Oreotrochilus chimborazo*; 16 = *Popelairia conversii*; 17 = *Thalurania colombica*; 18 = *Amazilia tzacatl*; 19 = *Campylopterus villaviscensio*; 20 = *Chlorostilbon mellisugus*; 21 = *Orthorhyncus cristatus*; 22 = *Lampornis clemenciae*; 23 = *Eugenes fulgens*; 24 = *Archilochus colubris*; 25 = *Myrtis fanny*; 26 = *Philodice mitchellii*; 27 = *Acestrura mulsant*. Vertical cells correspond to predictor variables: 1 = duration of breeding season; 2 = residual duration of breeding season (duration of breeding season regressed on male field masses obtained for this study); 3 = breeding seasonality; 4 = migratory behavior; 5 = number of congeneric species; 6 = residual number of congeneric species (number of congeneric species regressed on male field masses obtained for this study); 7 = male body mass; 8 = female body mass; 9 = average body mass; 10 = residual of male body mass (field masses obtained for this study regressed on midpoint of elevational occurrence); 11 = residual of female body mass; 12 = residual of average body mass; 13 = basal metabolic rate; 14 = residual of basal metabolic rate (metabolic rates regressed on corresponding masses from Bennett and Harvey 1987); 15 = mass-specific basal metabolic rate (based on corresponding masses from Bennett and Harvey 1987). Residual of mass-specific basal metabolic rate (mass-specific metabolic rates regressed on corresponding masses from Bennett and Harvey 1987) equivalent to 14 above. Results for number of congeneric species are qualitatively similar if based on analysis of one or both *Coeligena* species.

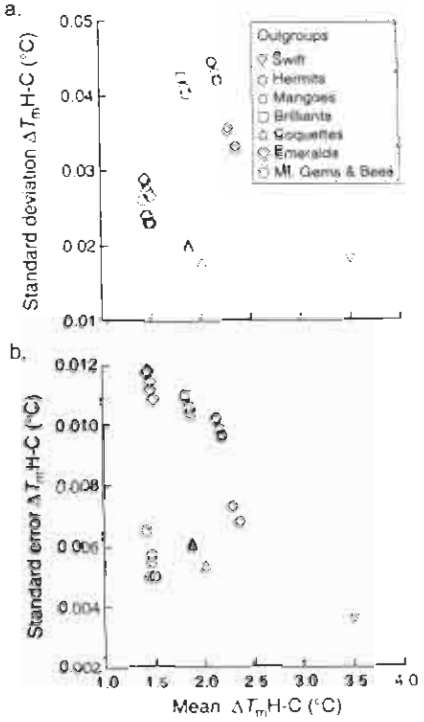

FIG. 4.—Scatter plot of standard deviation (*a*) and standard error (*b*) for log$_e$ genetic distance (ΔT_mH-C) for all outgroups, identified by the named clade to which they belong (see text for discussion).

times were lower than those for raw values, but even these conservative estimates remain highly significant over a broad range of outgroups. With few exceptions (always involving more terminal outgroups), correlations between measures of generation time or species diversity and path lengths were nonsignificant (and inconsistent in sign). For hermits, the much larger *Eutoxeres aquila* was evolving more slowly than *Threnetes ruckeri* (sign tests for ranked path lengths from each of the 24 nonhermits and the swift: $x = 0$, $n = 24$, $P \ll 0.0001$), though *E. aquila* also has a longer generation time and fewer (two as compared to three) congeneric species. Correlations between BMR (available for nonhermits only) and path lengths were inconsistent, bordering on (BMR, mass-specific BMR: one-tailed $P < 0.10$; Pearson) or attaining (mass-specific BMR only: two-tailed $P < 0.05$; Spearman) a significant positive correlation for some measures of metabolic rate (fig. 3).

The separate ANCOVAs subsuming each predictor variable (as covariate) and outgroup (as main effect) within a named clade (fig. 5; using either emeralds or mountain gems and bees as most terminal named clade of outgroups) indicate that path lengths are significantly associated with all measures of body mass (negative) and with mass-specific BMR (positive), but with no measures of generation time, species diversity, or mass-independent BMR (when calculations are possible; see fig. 3).

The significant mean effect of named clades no doubt reflects the appreciable shortening of distances from outgroups to ingroups imposed by the branching

Table 5
Cochran-Mantel-Haenszel Chi-Square Test of Linear Trends in Figure 3 with Mountain Gem and Bee Clade as Ingroup Only

Predictor	N	df	Pearson		Spearman	
			χ^2	P	χ^2	P
Demography[a]						
Linear trend[b]	126	1	**10.732**[d]	0.001	3.099	0.078
Mean row difference[c]		20	**23.145**	0.282	**41.477**	0.003
Body mass						
Linear trend	126	1	**6.074**	0.014	**72.877**	0.000
Mean row difference		20	**77.273**	0.000	**107.607**	0.000
Basal metabolism						
Linear trend	63	1	0.349	0.555	0.000	1.000
Mean row difference		20	4.438	1.000	0.000	1.000

[a] Cell values (see text) were combined across each measure of the general class (six for demography [four for generation time, two for species diversity], six for body mass, and three for basal metabolism) of predictor variable.

[b] Tests for linear association between the predictor (row) and outgroup (column) variables. Results are similar with mountain gems and bees as terminal outgroups. Cells with too few observations to calculate a correlation are scored as nonsignificant.

[c] Test of significant heterogeneity in frequency of nonsignificant and significant correlations.

[d] Bold values significant at indicated P value.

hierarchy of named clades within the phylogeny. The significant mean effect of a specific outgroup within a named clade is more difficult to interpret, because differences in mean distance to the same set of ingroups within each named clade can arise in two ways. One way is that different outgroup taxa may be evolving at different rates, which would affect all distances measured from that outgroup to the same set of ingroups. The other way is that experimental errors associated with extracting the DNA and labeling it with radioactive iodine may cause differences in melting temperatures among outgroup DNAs. As there is no replication of labels within outgroup species, such experimental effects cannot be separated by my analytical design. However, the lack of significant interaction between outgroup species and predictor variable indicates that the functional relationships between path lengths and predictor variables are very similar across outgroups within each named clade despite possible differences in label melting temperatures.

Discussion

The results of this study suggest that relative-rate tests based on path length distances give consistent results as long as outgroups capture a large number of ingroups. Over the range of distances and rates measured here, limitations imposed by autocorrelation and/or saturation effects seem less important, although comparisons more distant than those measured from the swift might reveal such effects. Given that relevant aspects of the biology of hummingbirds differ greatly from those of other vertebrates, I first discuss associations between relative rates and predictor variables in light of what is known about hummingbird biology, and then compare the results with those obtained for other organisms.

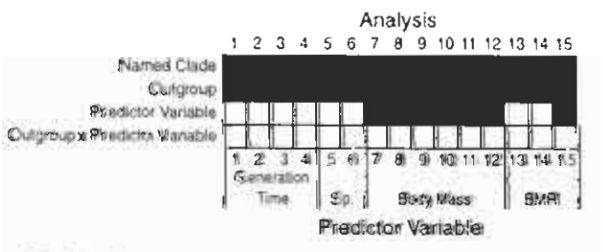

FIG. 5.—Schematic representation of results of nested ANCOVA for each row in figure 3. Notation is as in figure 3 (with black indicating two-tailed significance at $P < 0.05$), with emeralds as the terminal outgroup. Results are similar with mountain gems and bees as terminal outgroups except that small ingroup sample size prevented estimation of associations with metabolic rate.

Predictor Variables

The close parallel that often exists between generation time, metabolic rates, and body mass has made the task of separating their effects on molecular evolution difficult. Exceptions to their covariation have been noted in sharks, birds, and certain insects, where body mass and molecular evolutionary rate covary in the absence of corresponding differences in generation time (Martin, Naylor, and Palumbi 1992; Martin and Palumbi 1993; Rand 1994; Krajewski and King 1996). It is tempting to dismiss generation time as a cause of variation in rates of molecular evolution among hummingbirds simply because all species studied to date appear to breed in their first year (Bent 1940; Skutch 1972; Johnsgard 1983). However, even when such variation as may be present is considered, differences in generation time appear to be inconsequential.

A consideration of the extremes for generation time in the family also fails to support the hypothesis. For example, the tiny thorntail (*Popelairia conversii*) and bee (*Archilochus colubris* and relatives) hummingbirds (table 2 and fig. 2) probably have the longest generation times among trochilids as a consequence of their long-distance or elevational migrations, which absent them from the breeding grounds for most of the year (Johnsgard 1983; Hilty and Brown 1986). Indeed, males of these species adopt eclipse plumages that lack iridescent

patches and ornamental plumes for much of the year (Johnsgard 1983; personal observations), again suggesting that they breed only for a few months over the annual cycle. Contrary to the generation-time hypothesis, however, these species express some of the fastest recorded rates of molecular evolution among the hummingbirds examined (table 2 and fig. 2). In *Oreotrochilus*, by contrast, accelerated development of adult plumage, and possibly of breeding, is associated with one of the slowest rates of molecular evolution (table 2 and fig. 2). Finally, the young of lek-mating hermit hummingbirds may begin to attend mating aggregations (and potentially breed) as soon as 3 months after fledging (Stiles and Wolf 1979), but such hermits do not demonstrate an accelerated rate of molecular evolution (table 2; Bleiweiss 1998*b*, 1998*c*).

Although I failed to detect any relationship between species diversity and rates of evolution, the actual limits of monophyletic clades comprising taxa used in this study are still largely unresolved (Bleiweiss, Kirsch, and Matheus 1997). Possibly, then, the effects of species diversity on rates of molecular evolution in hummingbirds are not adequately tested by correlating rates with numbers of congeneric species, or at least not until more realistic generic limits for hummingbirds are determined. Additionally, hermit hummingbirds are almost an order of magnitude less diverse than nonhermits (Bleiweiss 1991), and the hybridization data suggest that the hermit rate is indeed significantly slower than that of nonhermits (table 2; Bleiweiss 1998*b*). Nevertheless, thorntails (fig. 2; *Popelairia*) are evolving more rapidly than any other clade in the phylogeny despite a species-diversity less than half that of brilliants or bees (table 2 and fig. 2). Conversely, the brilliant clade is as diverse or more so than the bees (Bleiweiss, Kirsch, and Matheus 1997), yet its molecular rate is much slower in comparison (table 2 and fig. 2). Thus, species diversity is unlikely to explain much of the variation in rates of molecular evolution among principal hummingbird clades, even given possible changes to generic limits.

The significant negative association between rate of DNA evolution and body mass documented here is inconsistent with the body temperature hypothesis, which predicts a positive association. On the other hand, the negative association between rate and body mass and the positive association between rate and mass-specific metabolism agree with the predictions of the metabolic-rate hypothesis (table 2 and figs. 2 and 3). However, evidence for a direct association between molecular rates and mass-independent metabolic rates is weaker, perhaps reflecting the small sample size and high levels of experimental error for the metabolic data (Bennett and Harvey 1987). Given these considerations and the close relationship between metabolism and body mass, the latter may be a more accurate predictor of the effect of metabolic rate on genomic evolution than are currently available experimental values of basal metabolic rate (Mooers and Harvey 1994).

Implications for Comparative Studies

Taken together, my results suggest that metabolic factors are important correlates, if not actual determinants of variation, in rates of molecular evolution in hummingbirds. These results differ from those obtained in several previous studies, including studies of birds, which have failed to support the metabolic-rate hypothesis (Adachi, Cao, and Hasegawa 1993; Mindell et al. 1996) or have supported body temperature (Mindell et al. 1996), generation time (Prager et al. 1974; Britten 1986; Sibley and Ahlquist 1990; Mooers and Harvey 1994), speciation (Mindell, Sites, and Grauer 1989; Barraclough, Harvey, and Nee 1996), or some combination of these other factors. Moreover, evidence for associations between metabolic and molecular evolutionary rates has been obtained largely for the DNA of mitochondria, whose rates of genomic evolution can be linked directly to their function in oxidative metabolism (Martin and Palumbi 1993). By contrast, DNA hybridization distances reflect mostly change in the single-copy nuclear DNA fraction.

The results for hummingbirds may reflect the exceptional biologies of these birds. Thus, hummingbird metabolism may be of sufficient magnitude (Suarez et al. 1991) to alter substitution rates even in the nuclear germ line. Moreover, hummingbirds appear to be exceptions to the general pattern of smaller-bodied species having shorter generation times; the relatively long generation times in small-bodied hummingbirds are probably caused by interspecific dominance patterns that force small-bodied species to emigrate to or from breeding habitat when nectar-based competition with larger hummingbirds increases. Finally, general constraints on hummingbird life history also may reduce variation in generation time and other demographic factors such that their effects on molecular evolution are obscured by the much larger effects of body mass. An appreciation that different mechanisms control rates of molecular evolution at different steps in the process of transcribing DNA into a functional protein also may help reconcile otherwise contradictory results across studies. For example, the body temperature hypothesis concerns functional constraints governing the effects of nonsynonymous substitutions, whereas the majority of substitutions measured by DNA hybridization data are probably synonymous.

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APPENDIX

Data for Predictor Variables Used in Analyses

Genus and Species	Generation Times[a]		Species		Elevation[b]		Field Mass[c]		Metabolism[d]	
	dbs	bs	mig	congen	min	max	M (*n*)	F (*n*)	B&H	BMR
Lampornis clemenciae	4	3	2	6	300	3,900	7.56 (8)	6.00 (1)	7.9	2.1
Thalurania colombica	5	3	2	6	0	1,900	4.68 (8)	3.83 (6)		
Aglaiocercus coelestis	12	1	1	2	300	2,100	5.94 (6)	4.33 (3)		
Coeligena wilsoni				10	700	2,000	7.18 (4)	6.38 (4)		
Eriocnemis luciani			2	10	2,800	4,800	6.30 (3)	5.90 (4)		
Eulampis holosericeus	5	3	1	2	0	600	6.01 (7)	5.30 (2)	8.4	3.2
Colibri coruscans	12	1	2	4	600	3,600	8.83 (10)	7.03 (7)		
Eugenes fulgens	9	3	4	1	900	3,300	7.10 (6)		6.6	2.1
Acestrura mulsant				5	1,500	2,800	3.75 (11)	4.05 (8)	3.3	1.6
Archilochus colubris	4	3	4	2	0	2,400	2.64 (8)	3.12 (2)	3.2	1.6
Myrtis fanny	12			1	1,200	2,800	3.18 (5)	3.40 (1)		
Philodice mitchellii			3	2	0	1,900	2.98 (2)	3.15 (1)		
Amazilia tzacatl	12	1	1	30	0	1,850	5.64 (8)	4.80 (4)		
Campylopterus villaviscencio				11	400	1,500	8.40 (1)	6.10 (2)		
Androdon aequatorialis				1	0	1,590	7.60 (3)	6.68 (6)		
Lesbia victoriae	9	3		2	2,600	4,000	4.99 (4)	4.25 (2)		
Doryfera ludovicae	7	3	1	2	900	2,700	6.81 (7)	6.70 (3)		
Oreotrochilus chimborazo	7	2	1	5	3,500	5,300	8.58 (10)	7.42 (4)	8.4	4.0
Heliodoxa jacula	7	3	1	9	500	2,300	8.83 (3)	8.20 (2)		
Heliothryx barroti	10	3	1	2	0	1,830	5.13 (3)			
Chlorostilbon melhsugus	8	3		13	0	2,200	3.05 (14)	3.18 (3)	2.9	3.0
Coeligena torquata	9	3	2	10	1,500	3,000	8.14 (8)	7.20 (2)		
Popelairia conversii	6	3	3	4	0	1,400	2.79 (7)	2.68 (6)		
Orthorhyncus cristatus	12	1	1	1	0	650	2.77 (3)	3.00 (1)	2.9	1.9
Threnetes ruckeri	5	3	1	3	0	1,050	6.56 (7)	6.39 (9)		
Eutoxeres aquila	6	3	2	2	0	2,100	10.55 (4)	9.36 (5)		

NOTE.—In two instances, data on predictor variables were available only for a congener of the species included in my study (generation time for *Oreotrochilus [estella,* not *chimborazo]* and BMR for *Eulampis [jugularis,* not *holosericeus]*). As those species are close relatives to the species in my study, any inaccuracies in these data may be minimal, and results of the analyses remained qualitatively similar whether or not the particular species was excluded from an analysis. I present the more inclusive analyses.

ABBREVIATIONS: dbs = duration of breeding season (in months; see text); bs = breeding seasonality (1 = continuous; 2 = accelerated [*Oreotrochilus*; see text]; 3 = seasonal); mig = migratory behavior (1 = sedentary; 2 = elevational migrant; 3 = pronounced elevational migrant; 4 = long-distance migrant); congen = number of congeneric species; min = minimum elevation (m); max = maximum elevation (m); field mass (g): M = average male mass; F = average female mass; B&H = mass (g) from Bennett and Harvey (1987); BMR = basal metabolic rate (resting metabolic rate; from Bennett and Harvey 1987).

[a] Literature sources: Carpenter (1976), Hilty and Brown (1986), Johnsgard (1983).

[b] Literature sources as footnote a and data compiled in Bleiweiss (1991).

[c] Unpublished field weights.

[d] Literature source: Bennett and Harvey (1987).

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Slow rate of molecular evolution in high-elevation hummingbirds

(Andes/DNA hybridization/molecular clock/oxygen metabolism)

ROBERT BLEIWEISS*

Department of Zoology and the Zoological Museum, Birge Hall, 430 Lincoln Drive, University of Wisconsin, Madison, WI 53706

Edited by Charles G. Sibley, Santa Rosa, CA, and approved November 6, 1997 (received for review August 18, 1997)

ABSTRACT **Estimates of relative rates of molecular evolution from a DNA-hybridization phylogeny for 26 hummingbird species provide evidence for a negative association between elevation and rate of single-copy genome evolution. This effect of elevation on rate remains significant even after taking into account a significant negative association between body mass and molecular rate. Population-level processes do not appear to account for these patterns because (*i*) all hummingbirds breed within their first year and (*ii*) the more extensive subdivision and speciation of bird populations living at high elevations predicts a positive association between elevation and rate. The negative association between body mass and molecular rate in other organisms has been attributed to higher mutation rates in forms with higher oxidative metabolism. As ambient oxygen tensions and temperature decrease with elevation, the slow rate of molecular evolution in high-elevation hummingbirds also may have a metabolic basis. A slower rate of single-copy DNA change at higher elevations suggests that the dynamics of molecular evolution cannot be separated from the environmental context.**

The initial view that molecular evolution proceeds at a steady or clock-like rate has given way to an appreciation that such rates may vary widely among organisms (1–3). A number of intrinsic biological attributes are known to be associated with deviations from clock-like rates of molecular evolution, including body mass, generation time, and population structure (4–7). Herein I present an analysis of published DNA hybridization data for hummingbirds (8) that indicates that rates of DNA evolution are slower in species living at higher elevations. Molecular adaptation to high elevations has been documented for a variety of molecules with specific physiological functions, hemoglobin, for example (9). As DNA hybridization measures change across the entire single-copy genome, however, the response of such a broad feature as rate of molecular change to an environmental parameter supports the generalization that DNA evolution is qualitatively similar to morphological evolution in that its form cannot be separated from the environmental context.

MATERIALS AND METHODS

Absolute rates of genetic evolution are difficult to obtain for hummingbirds because their fossil record is extremely limited (8). However, relative rates can be estimated by computing distances (fitted path lengths on the topology) from a designated "outgroup" taxon to members of a monophyletic "ingroup" with which it shares a common ancestor [relative rate test (10)], a procedure that avoids errors inherent in fossil calibrations of absolute rate. As a member of the sister group to hummingbirds (11, 12), the swift *Chaetura pelagica* provides an outgroup for relative-rate estimates among hummingbird species in both the hermit (Phaethornithinae) and nonhermit (Trochilinae) subfamilies (Fig. 1). In turn, any member of one hummingbird subfamily can serve as an outgroup for estimation of rates among species in the other subfamily.

As described in more detail elsewhere (8), the complete set of reciprocal median melting temperatures (T_m) for the 26 hummingbird species and outgroup swift were calculated from raw melting curves and then corrected in several steps to obtain the most accurate estimates of genetic distance (ΔT_mH-C) and phylogeny [ref. 8 and Fig. 1]. The hummingbirds included in the phylogeny represent all known principal lineages (Fig. 1) and reside at different elevations from sea level to over 5,000 m, reflecting the exceptional elevational diversification of hummingbird species during their evolutionary radiation (13). Of the two basal sister groups, nonhermits are an order of magnitude more diverse and occur over a much wider range of elevations than do the predominantly lowland tropical hermits (13). Consequently, nonhermits are better represented in the phylogeny (24 versus 2 species, respectively).

RESULTS

Associations. Previous comparisons of relative rates among the species examined herein have indicated significant molecular rate variation (14). More detailed comparisons based on the swift reveal that relative rates of evolution for the 24 nonhermits are significantly faster than for the two hermits (Wilcoxon two-sample test, $Z = 2.261$, $P < 0.0237$). The rates for hermits fall well outside both the normal distribution of rates for nonhermits (both subfamilies, Shapiro–Wilk $W = 0.835$, $P < 0.0005$; nonhermits only, Shapiro–Wilk $W = 0.967$, $P > 0.59$) and the 95% confidence interval of the regression of relative rates on elevation for nonhermits (Fig. 2); therefore, hermits appear to be distinct outliers for rates among hummingbirds and are analyzed separately.

For the 24 nonhermits, each of three measures of a species' elevational occurrence demonstrates a significant negative association with relative rates measured from the swift or from either of the two hermits (Table 1 and Fig. 2). The pattern is not caused by contributions from extreme outliers but expresses a consistent trend across the range of elevations occupied by hummingbirds. The same tendency obtains as well between the two hermits (Fig. 2) for relative rates measured from each of the 24 nonhermits (sign test, $x = 0$, $n = 24$, $P \ll 0.001$; Fig. 2). These consistent associations between elevation and rate are striking given the conservative estimates provided by relative rates, which discriminate only the independent terminal segments along the paths from the outgroup to the various ingroups.

A direct effect of elevation on rate of molecular evolution could be obscured by confounding variables such as generation

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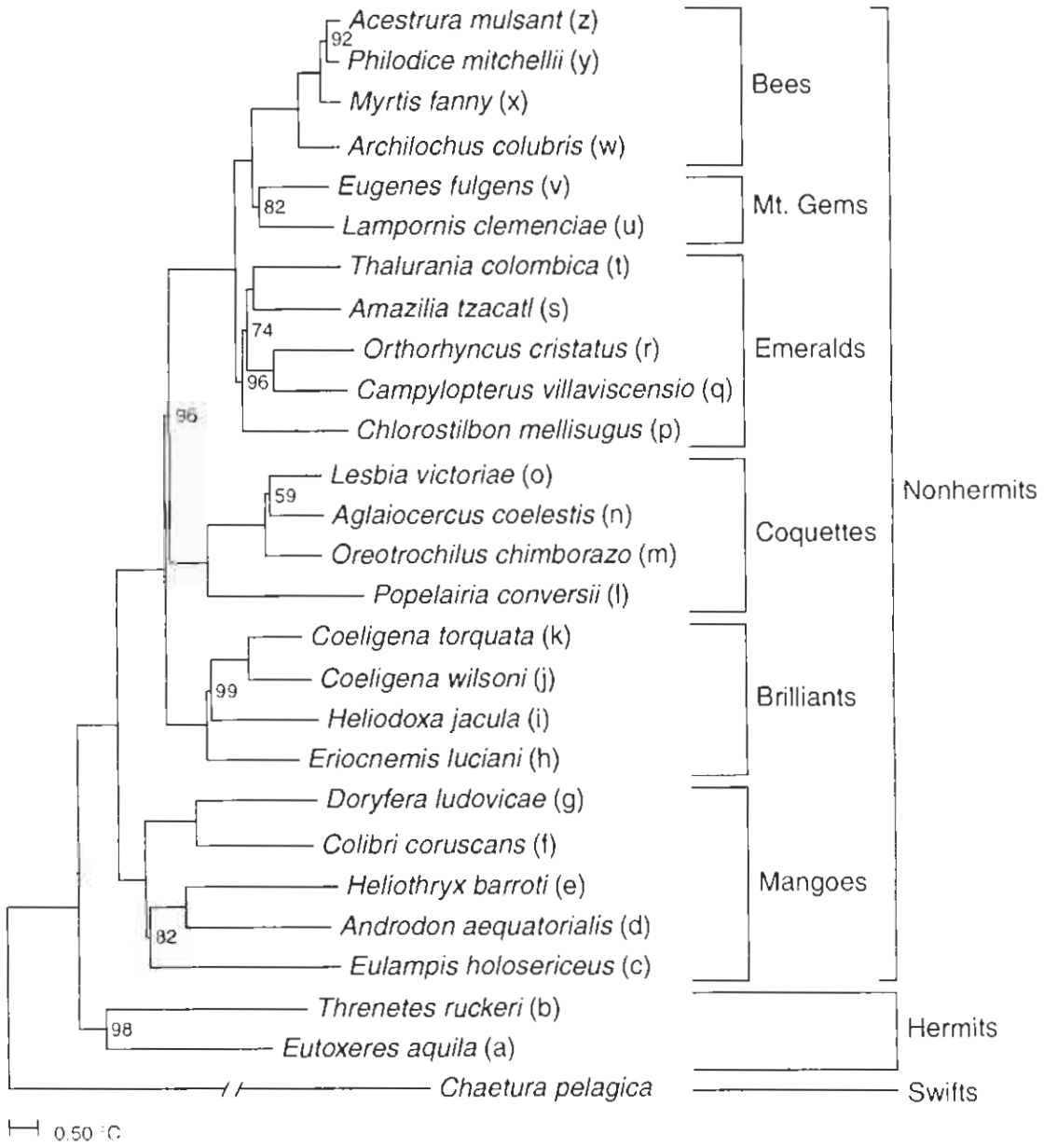

FIG. 1. Consensus unweighted least-squares FITCH topology obtained (8) from a complete matrix of symmetrized ΔT_mH-C values rooted with the outgroup swift *Chaetura pelagica*; names refer to principal nonhermit lineages and relevant subfamilies and families of the Apodiformes (hummingbirds and swifts), and letter codes to species as plotted in Fig. 2. The ΔT_mH-C index was obtained through several steps that minimize inaccuracies in distance measures (8). First, the T_{50}H index was obtained by correcting raw median melting temperatures (T_m) for normalized percentage hybridization (NPH) through application of the second-order polynomial found to fit observed values of T_{50}H regressed on T_m so as to avoid the excessive experimental error inherent in raw measures of NPH. The resulting T_{50}H values were multiplied by the empirically determined scaling factor of 1.2 for percentage sequence divergence (27) and then corrected for homoplasy (28). Finally, these distances were converted to so-called delta (Δ) values by standardizing the melting temperatures of different-species (heterologous) hybrids to the melting temperatures of same-species (homologous) hybrids (8). After symmetrization (29), average path lengths (12) for the resulting ΔT_mH-C values were estimated from 1,000 unweighted least-squares FITCH topologies (30) generated for a corresponding number of bootstrap pseudoreplicate matrices drawn from the complete matrix of 2,025 reciprocal genetic distances (three, rarely fewer, replicates per comparison). Internode support as indicated by bootstrap percentages (out of 1,000, if <100%) suggests strong support for the symmetrized topology, which was stable to multiple-deletion jackknifing (12). [Reproduced with permission from ref. 8. (Copyright 1997, Society for Molecular Biology and Evolution).]

time or body mass, both of which demonstrate negative associations with molecular rates in some vertebrate groups (5–7). With respect to generation time, all hummingbirds breed within their first year and variation in breeding age within this time frame is not significantly associated with rate variation (14). Alternatively, the decrease in rate with elevation could be an indirect consequence of selection for greater body mass in species living at higher and, hence, colder elevations (15). However, elevational occurrence is not correlated with body mass for hummingbirds in this (log$_e$ midpoint of elevational occurrence with log$_e$ male body mass, $r = 0.290$, $P = 0.1509$) or much larger (16) samples. Even after calculating the residuals of elevational occurrence regressed on (male) body mass to remove the effect of the latter, and then entering both variables in a general linear model (Table 2), partial F values support a statistically significant contribution to rate by elevation over one also made by body mass (Table 2).

Sources of Error. Statistically based comparative methods to account for nonindependence caused by phylogenetic relat-

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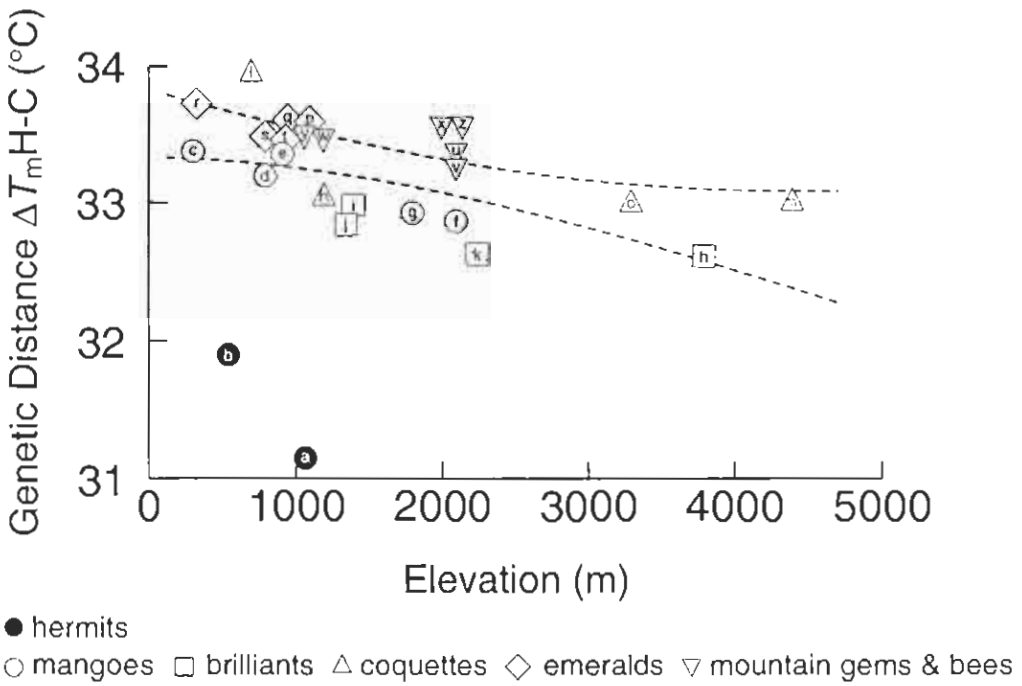

FIG. 2. Scatter plot of average path lengths to ingroup hummingbirds [Fig. 1; measured from outgroup swift (*Chaetura pelagica*)] versus midpoint of elevational occurrence. Taxa coded by principal lineage (symbol) and species (letter s as indicated in Fig. 1). Overlapping symbols moved to reveal letter codes. Dashed lines indicate the 95% confidence intervals for least-s es regression of nonhermits. Folded F tests indicate significantly less variation in fitted path lengths measured from swift compared with those measured from either hermit [$F' = 9.93$ (*Threnetes*), $F' = 11.48$ (*Eutoxeres*); $df = 23, 23$; $P < 0.0001$], consistent with autocorrelation and saturation effects for the more distant swift comparison. The two hermits give virtually identical results except that distances are uniformly shortened when the more slowly evolving *Eutoxeres aquila* is used as the reference taxon for relative-rate estimates.

edness are not developed for relative-rate tests (17). Consequently, I treated each taxon in the analysis as an independent data point, which artificially inflates the degrees of freedom for hypothesis testing. However, I failed to detect any significant difference in the association between rate and elevation among the different hummingbird lineages [when principal nonhermit lineage (as defined in Fig. 2) is added as a factor to the above model, interaction terms are not significant; for elevation, swift as outgroup, $F = 0.63$, $P > 0.65$; either hermit as outgroup, $F = 0.64$, $P > 0.64$]. Evidence that the negative association between rate and elevation occurs in different phyletic lines (Fig. 2) suggests that the overall significance of the pattern is not biased by relatedness among the taxa examined.

Table 1. Pearson correlation coefficients of ($\log_e$) elevational occurrence (14) with ($\log_e$) genetic distance [average path lengths, based on ΔT_mH-C (Fig. 1)] for the swift (*Chaetura pelagica*) and two hermits (*Threnetes ruckeri* and *Eutoxeres aquila*) as outgroups and nonhermits as ingroups (8)

Outgroup	Elevational occurrence*		
	Minimum	Maximum	Midpoint
Swift			
Chaetura pelagica	−0.6295	−0.5473	−0.5937
	0.0010†	0.0086	0.0022
Hermits			
Threnetes ruckeri	−0.6321	−0.5511	−0.5977
	0.0009	0.0053	0.0020
Eutoxeres aquila	−0.6322	−0.5510	−0.5977
	0.0009	0.0053	0.0020

All probabilities are two-tailed.

*Minimum, lowest elevational occurrence; maximum, highest elevational occurrence; midpoint, midpoint between minimum and maximum.

†Analyses were performed in SAS for UNIX on a SPARC station 20. All P were less than 0.05 after Bonferroni correction for $n = 3$ simultaneous comparisons.

Both empirical and analytical considerations also suggest that observed variation in path lengths reflects variation in rates and not biases in experimental error or differences in genome structure. Melting temperatures of same-individual hybrids of each species used to calculate genetic difference (ΔT_mH-C) values for distance-matrix construction (see caption to Fig. 1) are free from variation caused by rate or evolutionary relationship, thereby providing a direct measure of the variation contributed by fragment length or base composition. Lack of significant correlations between same-individual hybrid melting temperatures and independent variables (e.g., $\log_e$ male body mass, $r = -0.0134$, $P = 0.948$; $\log_e$ midpoint of elevational occurrence, $r = 0.1306$, $P = 0.525$) suggests, therefore, that contributions by these other sources of variation are small and/or random with respect to the focal rate patterns. Furthermore, scaling of the data to the average homologous melting temperature (symmetrization; see caption to Fig. 1) before estimation of path lengths ameliorates the effects of variation in homologous melting temperatures [e.g., compression of distances (8)] and of unequal Δ values between reciprocal comparisons, which may arise from differences in genome size. Thus, the negative association between elevation and rate of molecular evolution appears robust to possible confounding influences.

DISCUSSION

Evidence for slower rates of single-copy DNA evolution in higher-elevation hummingbirds has a number of important implications for studies of organismal and molecular processes. The effect of elevation on rate implies that general features of molecular evolution depend on the physical environment, a connection attributed traditionally only to morphological traits. Moreover, calculations of divergence times based on the assumption of a molecular clock will underestimate the ages of

Table 2. General linear models with residual midpoint of elevational occurrence (RMIDEL; ref. 14) and male body mass (MALEM; ref. 14) as independent variables and genetic distance from outgroup to nonhermit ingroups [average path lengths, based on ΔT_{50}H-C (Fig. 1)] as dependent variable

Outgroup Source	*df*	Type III sum of squares	Mean square	*F* value	$P > F$
Swift					
Chaetura pelagica					
RMIDEL	1	0.000338	0.000338	7.22	0.0138*
MALEM	1	0.001108	0.001108	23.61	0.0001
Error	21	0.000985	0.000047		
Corrected total	23	0.002550			
Hermits					
Threnetes ruckeri					
RMIDEL	1	0.003456	0.003456	7.44	0.0126
MALEM	1	0.010913	0.010913	23.48	0.0001
Error	21	0.009760	0.000465		
Corrected total	23	0.025323			
Eutoxeres aquila					
RMIDEL	1	0.003998	0.003998	7.43	0.0126
MALEM	1	0.012603	0.012603	23.44	0.0001
Error	21	0.011293	0.000538		
Corrected total	23	0.029274			

For all models, interaction terms of covariates with lineage membership included in error term. Separate analyses were conducted for each outgroup to maintain independence of the tests, which all are based on the same set of ingroup species. Alternative measures of elevational occurrence (Table 1) and body mass (female, species average; ref. 14) gave the same qualitative results. All data are log-transformed.

*Analyses were performed in SAS for UNIX on a SPARC station 20. All P were less than 0.05 after Bonferroni correction for $n = 3$ simultaneous comparisons.

high-elevation clades relative to ones found at lower elevations. The relationship between the amount of genetic and phenotypic change may be altered as well. Recognition of these biases is important especially for studies of speciation in montane regions, which typically emphasize the relative youthfulness and explosive diversification of high montane forms. Thus, evolutionary studies must consider that genetic dynamics at high elevations may operate differently than in other geographic settings.

The present study adds elevation to the growing list of influences on rates of molecular evolution. However, it is unclear to what extent the underlying mechanisms differ among these many correlates of rate. The negative association between rate of molecular evolution and elevation is counter to expectations that increased subdivision and geographic speciation among high-elevation populations should translate into greater genetic differentiation (4, 18). Moreover, as all hummingbirds breed in their first year, variation in generation time is not likely to be the cause of rate variation in these birds (14). On the other hand, DNA hybridization distances probably reflect mutation rate because they derive from the entire single-copy genome. Thus, the decrease in rate with elevation could reflect a reduced mutation rate caused by physical conditions at high elevations.

The extraordinary physiologies of hummingbirds suggest that metabolic factors could affect mutation rates. Indeed, the negative association between body mass and molecular evolutionary rate documented herein has been explained for mitochondrial DNA as a response to metabolic rate via the mutagenic effects of oxygen (5–7). Although most of the DNA indexed by DNA hybridization represents the nuclear fraction, mitochondria are the primary source of free radicals that damage DNA everywhere in the body (3), and they are present at extraordinary densities in the striated muscles that form the bulk of a hummingbird's mass (19). Thus, free-radical flow caused by mitochondrial activity could increase mutation rates in the nuclear genomes of hummingbirds.

As a starting point for future studies, I suggest that the changed physical conditions at higher elevations (20) could lower mutation rates in resident hummingbirds either because lower partial pressures of oxygen limit maximum oxygen consumption (21) or because lower temperatures require hummingbirds to enter a state of physiological torpor more frequently and at a lower body temperature for a given body mass (20), or both. Lower oxidative stress also might arise as a consequence of reduced caloric intake (22) through the consumption of more dilute nectars typical of higher-elevation bird-pollinated plants (23). An additional factor to consider is that many montane hummingbirds cling rather than hover while feeding at flowers (24, 25). This behavioral response at high elevations also may reduce overall oxygen consumption. However, typical hover feeders occur at moderate to high elevations (*Doryfera ludoviciae* among mangoes and *Cocligena torquata* among brilliants) and even these species are evolving more slowly than related low-elevation forms (Figs. 1 and 2). Thus, the molecular response to high elevations occurs independent of flight methods.

Whatever its cause, environmental correlates of molecular evolutionary rates may prove widespread, because birds and other homeotherms living at higher latitude often have greater body mass (15), which as documented herein and in a variety of organisms, demonstrates a negative relationships with rate. Moreover, the influence of mutation rates on demographic processes of aging and mortality (26) may impose characteristic evolutionary dynamics in populations living at different elevations and/or latitudes or in different atmospheres (paleoenvironments with more or less oxygen). Further study of the interaction of population and molecular processes in different environments may reveal previously unsuspected phenomena.

I thank John A. W. Kirsch for assistance in the laboratory, John A. W. Kirsch, Dana H. Geary, and two anonymous reviewers for comments on the manuscript, and William J. Feeny for drafting the figures. Additional acknowledgments of logistical and financial support for this work are detailed elsewhere (8).

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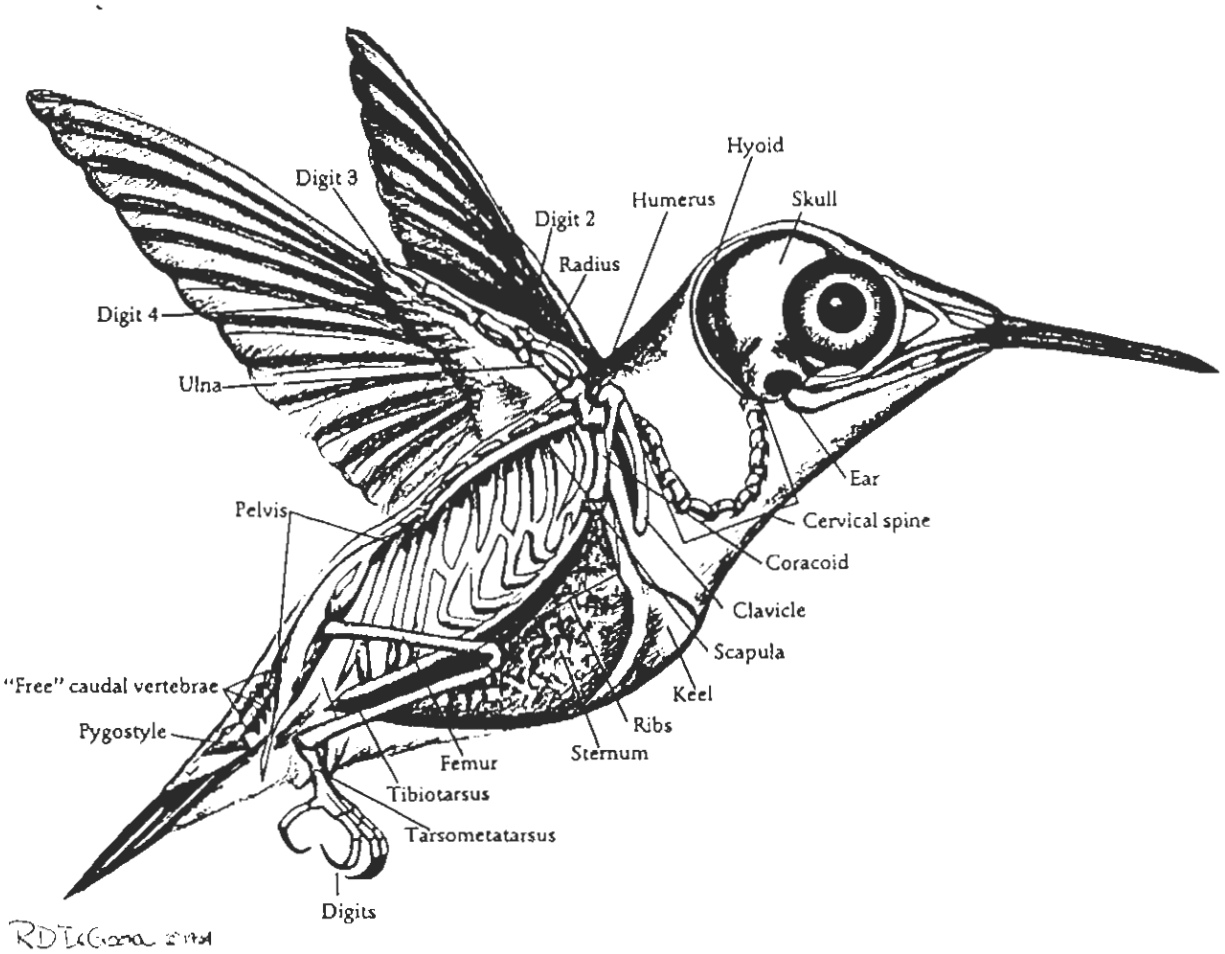

(Thought you'd like to see what one actually looks like. - ed.)

US Geological Survey
Midcontinent Ecological Science Center
4512 McMurry Ave.
Fort Collins, CO 80525-3400

December 2, 1998

(970) 226-9471
226-9230 (FAX)
gordon_rodda@compuserve.com

The Conservation Agency
6 Swinburne St.
Conanicut Island, RI 02835

Skip,

Thanks again for the wonderful month of October! I have sent the paper off to Nature. I expect that we will know whether they are taking it seriously or not before Christmas. As you see from the enclosed cover letter, Nature puts some pretty severe restrictions on manuscripts. Perhaps the most painful was that for the suitable category, Scientific Correspondence, they do not allow acknowledgments. I even tried to hide acknowledgments in a footnote, but they expressly do not allow that. Therefore, there seems to be no way to properly credit yourself, the volunteers, Henry, the Falconwood Foundation, or the Conservation Agency. Rest assured that this omission will be redressed in the report and technical publications that arise from this work, but there just doesn't seem to be any way to do it here.

Another constraint that Nature applies to Scientific Correspondence is that one is limited to 500 words, 1 fig., and 10 citations. Therefore, much has been omitted. Again, this will be corrected in the full versions.

Yet another constraint is that they insist on a press embargo until publication. I finessed this slightly in the cover letter (enclosed) by correctly noting that the media has not publicized this and we have not "discussed" this with them (I didn't say that an attempt was not made to bring it to their attention). If you are interested, I will be happy to send you the full details of the press embargo, but essentially we are allowed to mention the results as much as we want to other scientists, but we are not supposed to talk to the media or post anything on a web page.

I'll let you know if we get anything positive from Nature, or if we give up entirely. If this flies, there will be an opportunity for publicity concurrent with publication. Keep your fingers crossed.

Cheers,

Gordon

US Geological Survey
Midcontinent Ecological Science Center
4512 McMurry Ave.
Fort Collins, CO 80525-3400

December 2, 1998

(970) 226-9471
226-9230 (FAX)
gordon_rodda@compuserve.com

Nature
968 National Press Building
Washington, DC 20045-1938

To whom it may concern,

Enclosed are three copies of a proposed contribution for Scientific Correspondence. It reports the discovery in October of a diurnal gecko population in the Virgin Islands, the density of which exceeds that of all previous terrestrial vertebrate records by a factor of about three. Not only is this discovery a landmark for the field of ecology, but we think it will be of general interest to the public. Most people express awe and an abiding curiosity about high density populations, yet ecological knowledge of these is unquantitative and unpredictive. The fact that such a high density of vertebrates has remained overlooked, well into the era of space travel, also says something important about the prevailing level of biological ignorance about our planet.

Reviewers who have read this manuscript have expressed an interest in seeing what the creatures look like. I have in my possession extremely sharp (f32) 35 mm slides of them, which are available upon request. Machine copies of two of these are enclosed for your edification. The submitted manuscript, however, relies on only one figure, as is specified for Scientific Correspondence.

The authors have no related papers submitted. We anticipate that the full technical details of this work will eventually be prepared for submission to a specialist journal, but such a submission will not take place until the Nature manuscript has been fully processed. The main finding reported in this paper has been discussed at two scientific presentations (one on Tortola Island, British Virgin Islands on 27 Oct; the other at Texas A&M on 12 Nov.), but has not be publicized in the press or discussed with the media. We will not do so, pending your decision. We see no need to accompany this article with Supplementary Information.

We look forward to your review of this manuscript.

Sincerely,

Gordon Rodda

Gordon Rodda

The densest terrestrial vertebrate

Ecologists seek to understand the distribution and abundance of plant and animal populations. High animal densities often result from localized aggregation. Social animals, such as wildebeest, may be dense in one area because they have vacated another. Non-social species may aggregate because suitable habitat is very restricted in distribution (e.g., rattlesnakes at a wintering den). However, non-aggregating species are most often found at low densities. Exceptions to this generalization shed light on the conditions that favor survival and reproduction. Here we report one such exception, a species that greatly exceeds the densities reported for all other non-aggregated terrestrial vertebrates.

Our study was conducted on Guana Island, British Virgin Islands. We censused the vertebrates and the vegetation of four 10 x 10 m plots, two each in representative stands of early successional (legume: *Acacia/Leucaena*) and mid-successional (seagrape: *Coccoloba*) forest. To insure that vertebrates did not enter or leave the plots during counting, the foliage outside of each plot was trimmed to separate it from the plot vegetation by 1.5 m. Movement of animals at ground level was blocked by a 50 cm tall fence of aluminum flashing that was coated with a spray grease to repulse climbing species. The fence was buried in the ground 5-10 cm to block the movements of opportunistically burrowing species. Fencing and trimming was done at night, during the species' inactive period, to minimize displacement of plot occupants and avoid an undercount. In the following days we captured all non-flying aboveground vertebrates in the isolated plots by carefully examining and removing all aboveground vegetation.

Overall we collected 7 snakes, 1401 lizards, and no amphibians, birds, or mammals. Most (94.5%) of the lizards were *Sphaerodactylus macrolepis*, a diminutive gecko, associated with deep, moist leaf litter[1]. The large leaves of seagrape provide suitable litter. Of 20 vegetation monitoring stations in the two legume plots, the percentages having litter at least 1 cm deep were 0% and 70%; these plots housed 6 and 262 *S. macrolepis* respectively. In contrast, the two seagrape plots were predominately (75%) or almost completely (95%) covered with deep leaf litter, and these plots had 380 and 676 geckos, respectively.

We project that the gecko attains densities of around 67,600 ha^{-1} in areas having continuous seagrape leaf litter, and may average 52,800 ha^{-1} in typical seagrape forest. Either of these values far surpasses reported densities of non-aggregated terrestrial vertebrates. A landmark study[2] of leaf litter salamanders (*Plethodon cinereus*) in New Hampshire documented densities of around 2950 ha^{-1}. The highest known density of frogs (20,570 ha^{-1}) is for the leaf litter foraging species *Eleutherodactylus coqui* in Puerto Rico[3]. Prior to this study, the highest reported density of lizards (23,600 ha^{-1}; Fig. 1) was for the arboreal anole *Anolis stratulus*, also in Puerto Rico[4]. No mammals or birds are known to approach these high densities[5,6].

Two common features unite the reigning high density representatives of these groups: they occur in leaf litter (frogs, salamanders, and now lizards), and they are small. Mean masses are below 1 g for each of the species, and the geckos averaged only 0.285 g. Nonetheless, the geckos' mean biomass of 15.2 kg-ha^{-1} in seagrape exceeds that reported for African elephants (5.5 kg-ha^{-1} in Gabon[7]; 12.9 kg-ha^{-1} in West Africa[6]). Unlike elephants, however, the geckos are likely to be overlooked by a casual observer.

Gordon H. Rodda

USGS Midcontinent Ecological Science Center

4512 McMurry Ave.

Fort Collins, Colorado 80525, USA

email: Gordon_Rodda@compuserve.com

Gad Perry

Ohio State University

P.O. Box 8255, MOU-3

Dededo, Guam 96912-8255, USA

Renée J. Rondeau

Colorado Natural Heritage Program

Colorado State University

254 General Sciences Bldg.

Fort Collins, Colorado 80523, USA

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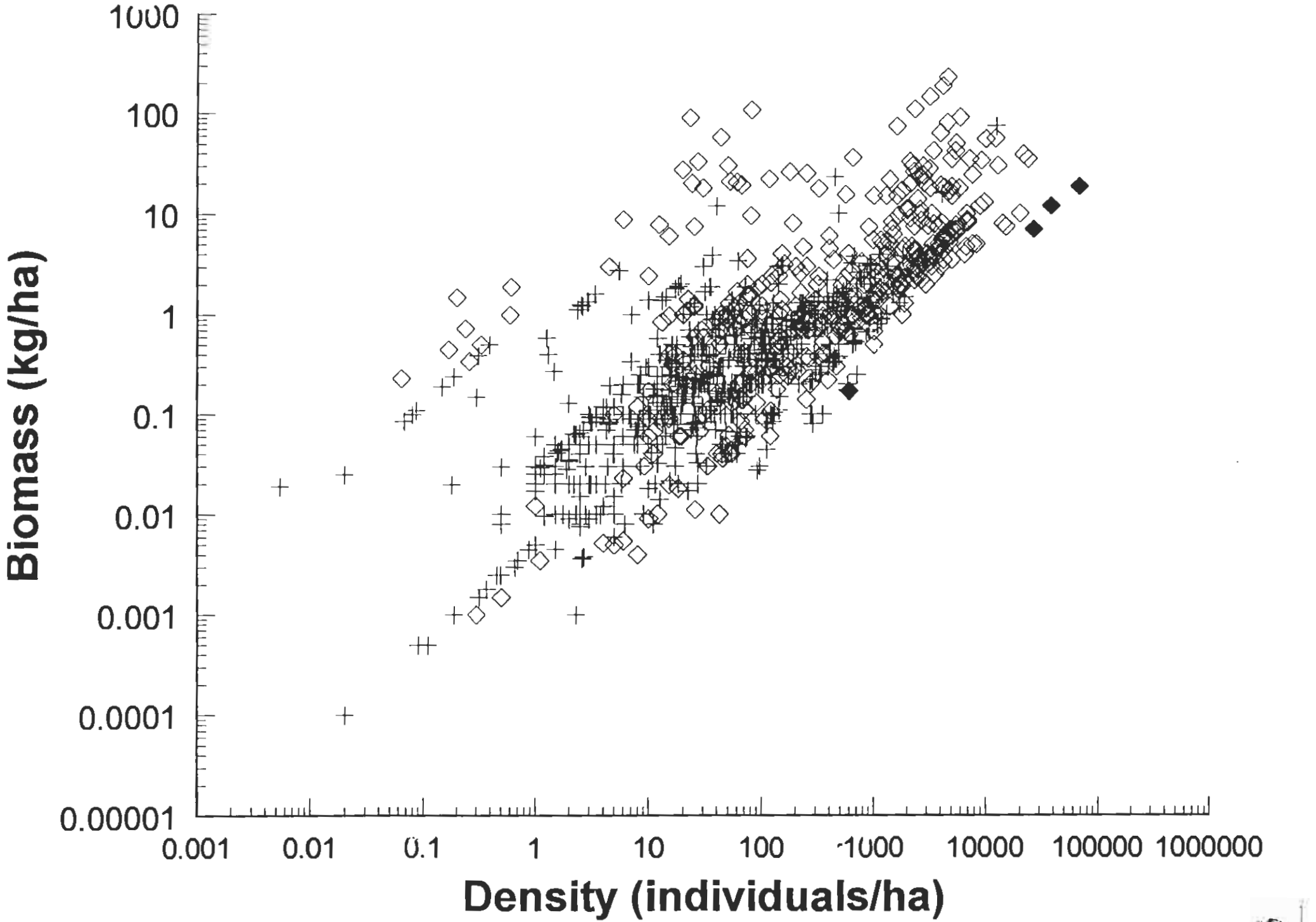
Caption to figure

Figure 1 Density estimates of 1072 non-aggregated lizard species*venue combinations taken from our work and 228 literature sources (available upon request). Values marked with a + are from mainland sites; the others are from islands. The four closed symbols represent the *Sphaerodactylus macrolepis* samples reported here.


1000
100
10
1
0.1
0.01
0.001
0.0001
0.00001
Biomass (kg/ha)
0.001
0.01
0.1
1
10
100
1000
10000
100000
1000000
Density (individuals/ha)

Dwarfs, Giants, and Rock-Knockoffs: Evolution of Diversity in Antillean Anoles

by
James (Skip) Lazell

The Conservation Agency, 6 Swinburne St., Jamestown, RI 02835
jcinjtown@aol.com

I have long agreed with the orthodox neo-Darwinian view that new species evolve from populations peripherally isolated from their parental stocks, in the Antilles by the simple, repetitive process of interglacial sea level rise. Thus, the new species are "daughter" species of their ancestral stocks, not "sister" species. Separate-but-equal dichotomous branching never occurs. The ancestral species remain essentially unchanged unless or until the new species invade the parental range, typically as a result of glacial maximum sea level drop. Then the opportunity for classic Darwinian character divergence emerges.

The ideal structure for speciation in isolation is a rock: a sheer-sided formation that, at interglacial high-stand sea level, is pounded by surf and provides scant or no opportunity for over-water waif dispersers to colonize and retard the speciation process by adding parental species genes. However, few anole populations stranded on such rocks persist and survive to evolve into new forms. On the Puerto Rico Bank, for example, at least four species of anoles were able to spread virtually throughout the area occupied by today's Virgin Islands at Wurm glacial maximum, 10-20 kya: Anolis cristatellus, A. stratulus, A. pulchellus, and A. roosevelti. It is highly probable that more species from Puerto Rico proper dispersed overland at glacial maximum into the Virgins area too, but if so none survived into historical times.

One of the four species, A. roosevelti, may now be extinct as a result of artificial, post-Colombian deforestation. Two, A. stratulus and A. pulchellus, have not survived on any of the several small islets that qualify as rocks. At least five islets qualify as rocks in my terms (and are locally called that): Carrot, Carval, Cockroach, Sail, and Watson. Of these, only Carrot and Cockroach seem to harbor anoles today, in both cases derivatives of Anolis cristatellus wileyae. One of these, A. ernestwilliamsi of Carrot Rock, is well differentiated and has occasionally colonized adjacent Peter Island to survive (however briefly) in sympatry with A. c. wileyae, its parental stock. Cockroach Rock anoles are less obviously differentiated from A. C. wileyae but the few available specimens are unusually large, short-headed, and big-scaled. This population is certainly worth a closer look.

Dry rocks present a strong selection pressure for water retention, and this can be augmented by large size. Thus, dry rocks like Carrot and Cockroach may produce incipient giants. Wet rocks might present an opportunity for dwarfism, if small size was advantageous in the absence of selection for water retention. However, wet rocks -- that is, wet with fresh water -- are hard to find. There are a couple off the windward coast of Dominica that may repay investigation.

Long ago (Copeia 1964: 716-718) I suggested that Anolis gingivinus on Sombrero might undergo rapid speciation, but Ellen Censky tells me that population has apparently winked out. The nearby Anguilla Bank provides some outstanding prospects for rock-knockoffs. I never got to Pain de Sucre off St. Barts in the course of my field work of 30-40 years ago. Apparently no one else has reached it since. Most amazing is the remotely isolated La Poule and Les Poussins cluster far northwest of St. Barts. These are called "The Groupers" on tourist maps. I plan to make a try for these islets in the near future, before I get too stiff to climb.

But why me? Are there not others, far younger and more agile, who have thought of potential speciation in isolation too? Well, if one of you gets there before me here, are some predictions:

On the wet rocks off Dominica I expect small anoles with big scales. In Anolis oculatus, scale size seems to correlate positively with moisture.

On the dry rocks near St. Barts I expect relative giants (parental A. gingivinus is relatively small), but I cannot guess scale size. Indeed, the relationship of scale size to water seems reversed in some forms, like A. ernestwilliamsi. We need a good integumentary physiologist to look into this problem.

How does one know if there are no anoles surviving? Spiders. Small salticid or attid jumping spiders and little, plump orb weavers like Argiope argentata are densely abundant on islets lacking anoles (thanks, Tom Schoener, for pointing that out). If you find lots of spiders there probably are no anoles.

The race is on. Good luck.

In press, 20.iv.99:
Anolis Newsletter

On the Rocks

The Anegada rock iguana is not a handsome animal. The gray lizard can grow up to 5 feet long and has a pronounced spike running down its back. So why are some people on this small British Virgin Island trying so hard to save it?

As it turns out, the rock iguana, indigenous only to Anegada, is seriously endangered. A recent study showed only about 200 remain on the island in the wild. And this particular type of iguana is — in iguana circles — historically significant. It's considered to be the so-called "mother species" to many subspecies of iguanas found in the Caribbean basin, according to Cleveland Sam, a spokesman for the BVI's National Parks Trust.

The trust, with funding from the British Foreign and Commonwealth Office and the World Wildlife Fund, has embarked on a year-long study of the iguana and an extensive attempt to save the species. To this end, the trust has built a facility dubbed Head Start, where juvenile Anegada rock iguana can be raised without being preyed upon by their No. 1 nemesis: feral cats.

In addition to the Head Start facility, the trust is preparing an environmental campaign that will be distributed to BVI schoolchildren, training senior staffers on iguana husbandry and looking into the feasibility of eradicating stray cats.

"These lizards are a very, very ugly animal," says Sam. "But they are still an important species."

Leaping lizards: The cause of the Anegada rock iguana has received international support.

Herpetologica 55(1): 1999, 7–17

EFFECT OF INTRODUCED UNGULATES ON DENSITY, DIETARY PREFERENCES, HOME RANGE, AND PHYSICAL CONDITION OF THE IGUANA (*CYCLURA PINGUIS*) ON ANEGADA

NUMI C. MITCHELL

The Conservation Agency Branch Office, 67 Howland Avenue, Jamestown, RI 02835, USA

ABSTRACT: I examined distribution, population density and structure, diet, habitat use, home-range dynamics, and physical condition of the Anegada population of *Cyclura pinguis* using ground surveys, interviews with residents, mark-and-recapture estimates, fecal analysis, feeding experiments, radiotelemetry, and life-history data. When compared with a study of 1968, the density of the extant population at a 43-ha study site was 0.36/ha, as opposed to 2.03/ha. Leaves represented only 38% of dietary volume, in contrast to 71% in 1968. Fruit comprised 56% of the diet. Well fed individuals of *C. pinguis* from a relocated population on Guana Island would not eat the leafy components of the Anegada iguanas' diet. Home ranges on Anegada overlapped and were 100 times larger than previously recorded. The sex ratio was two males to one female as opposed to 1:1 in 1968. Iguanas had proportionately lower body mass than animals captured in 1968. Population decline on Anegada seems largely due to increased competition from live stock, managed in 1968 but now feral, eating most palatable vegetation from the understory. Predation by cats and dogs is also a threat. The total remaining population is estimated at <200 individuals. A national park designed to protect the endangered population of *C. pinguis* has been proposed for Anegada.

Key words: Iguana; *Cyclura pinguis*; Population density; Home range; Diet; Competition

FOSSILS from caves in Puerto Rico (Pregill, 1981) and Indian kitchen middens from St. Thomas (Miller, 1918) show that *Cyclura pinguis* (taxonomy follows Sites et al., 1996) was once widely distributed on the Puerto Rico Bank. Predation pressure by humans, domestic dogs, and cats likely reduced the range to Anegada, British Virgin Islands, a 4000-ha island at the northeastern extent of its historic range. Anegada's densely spaced escape retreats provided by the porous limestone and low human population may explain why the lizard survived there.

In areas of Anegada where iguanas are most numerous, several species of trees, typically *Coccoloba uvifera* (sea grape), *Acacia anegadensis* (pokemeboy), *Pisonia subcordata* (loblolly), and *Ficus citrifolia* (strangler fig), colonize scattered small holes or fissures in the cap-rock. As these trees grow, their roots conduct rainwater

into the limestone, which dissolves solution holes in the already porous underlayers of rock. With further growth, their roots begin to crack and uplift the rock around them, sometimes in large plates. Windblown soil and organic matter are trapped by the irregular surface, which improves the habitat for the established plants there as well as for new colonizers. Solution holes associated with the trees continue to dissolve into large pits or caves. This successional scenario creates islands of habitat distinct from the surrounding scrub that support iguanas. Their refuges are found beneath the trees, under limestone slabs, or in the solution pits. Iguanas occupying these areas may deposit scats containing viable seeds of food plants (Iverson, 1985), which might further improve the habitat. In northern areas of the cay, where iguanas have always been most abundant, there are densely spaced limestone retreats, greater soil depths, and relatively diverse woodlands. The north coast provides an abundance of sea grapes (*Cocoloba uvifera*), in late summer and autumn, as well as sandy nesting habitat.

Over the past few decades, the population of *C. pinguis* has declined on Anegada. Carey (1975), in a 3-mo ecological study of *C. pinguis* in 1968, found indications that the population was senescent. He suggested that grazing livestock competed with the iguanas on Anegada and represented the primary threat to the species. Grazing ungulates were much less numerous than they are now. Stock animals were usually kept separate from agricultural crops and the rest of the island by an elaborate network of stone walls. Shortly after Carey's field-work was completed, walls were bulldozed to create new roads and an airstrip. Stock animals could not be restrained, escaped to the brush, and were left untended. Goats, cattle, donkeys, and sheep now roam the entire cay and breed to carrying capacity, as evidenced by their emaciation and starvation.

During this study, I made assessments of iguana distribution, population density, home-range size, patterns of burrow-use, and dietary selection. I used food-selection experiments to compare the diet of iguanas on Anegada with that of a relocated population of *C. pinguis* on Guana Island, a 300-ha island lying north of Tortola. Though Guana is within the historic range of the species, the iguana population there is derived from eight individuals moved from Anegada between 1984 and 1987 by James Lazell. Guana Island differs from Anegada in being volcanic in origin and, until 1993, in having only one feral grazer, sheep, which has overgrazed the island extensively. Part of the island has traditionally been surrounded by a sheep-excluding fence, a unique situation that allowed me to examine dietary preferences of iguanas inhabiting areas with no feral ungulates (Goodyear and Lazell, 1994).

I found that the experience of local residents was valuable for comparing historical and present distribution and abundance of iguanas, identifying potential causes of population decline, assessing qualitative changes in the vegetative communities, and evaluating habitat quality for iguanas. I used information from five lifetime residents of Anegada who had spent much of their lives in the bush (hunting, tending livestock, fishing, or collecting salt at the ponds): one 40, one 60, and three approximately 80 yr old. Information was found to be quite consistent between reports and provided a useful perspective of the species' status since the 1940's.

Methods

On Anegada, field work occurred during May and June 1988, May 1989 through January 1990, March through October 1990, and March 1991, October 1993, and March 1994; and on Guana Island each October from 1990 through 1993. Details of home-range size, movements, and burrow use are described for iguanas on Guana Island by Goodyear and Lazell (1994).

Density Estimates

Information on the historical status and population centers of *C. pinguis* on Anegada was provided by residents of Anegada and by Carey (1975). Ground survey work was done to determine presence, absence, and general abundance of the species. Pri-

FIG. 1.—Historical (1930–1979, left of arrow) and present densities (1980–1993, right of arrow) of *Cyclura pinguis* on Anegada. In locations showing single estimates (those without arrows) densities have not changed. H = high, M = medium, L = low, O = occasional individuals, X = no individuals, a = adults, j = juveniles, b = both. The 12.5-ha study area in which animals were captured, marked, and released, is shown.

mary indicators of iguana presence were tail-drags in sand or soil, feces, holes with worn or muddy entryways, or visual observation. Information on diet, home-range size and movements, and an estimate of population size was obtained from individuals in a 12.5-ha study area in the Bones Bight-Low Cay area (Fig. 1). Captured individuals were toe-clipped prior to release and could be recognized at close range. Radiotagged individuals could be recognized visually from afar by the color of their transmitter belts.

Iguanas were captured by hand, with nooses placed at burrow entrances, or with box traps baited with fruit. Following the methods of Goodyear and Lazell (1994), I defined the perimeter of the 12.5-ha study area to be the outermost points of "capture" or "recapture" of iguanas. Animals were recorded to have been "captured" or "recaptured" if trapped or observed but, because radiotags positively biased chance of recapture (violating the assumption of equal chance of capture required for mark-and-recapture estimates), observations of radio-located individuals were not. For density estimates, a boundary strip equal to the average home-range radius of all radiotagged individuals was added to the study area, to account for animal movements on and off the study area and to approximate the total area sampled (Dice, 1938; Goodyear and Lazell, 1994). After water (ocean and salt pond) overlapping the boundary strip was subtracted, the total sampling area was 42.6 ha. Density estimates were made with the Schnabel (1938) method using the SCHNABEL program (Krebs, 1989). To derive an approximation of the total population on Anegada, I ranked all regions of the island relative to the study area, which now has the highest iguana density found on the island. I assigned regions to one of four roughly defined categories: density equivalent to the study area, density ¾ that of the study area, density ¼ that of study area, or areas without iguanas. I tallied land area in each category, calculated population estimates for each, and summed the estimates for total population size.

Diet Study

On Anegada, dried feces were analyzed and plant species ranked by percent of volume. On Guana, I conducted a series of feeding experiments using foods known to be consumed by iguanas on Anegada. In an experimental session, iguanas were pre-

sented with an array of potential food items. Items of unknown quality were interspersed randomly with grapes (*Vitis*, a favored food) to maintain the animals' interest. Foods were tossed to iguanas at a range of 2 m or less. Animals' responses to items were scored only if items were noticed (reflected by a downward shift of the eyes to the items as they landed) and if iguanas would take and eat favored food items after the trial. Items were scored as eaten, tasted and rejected, or ignored.

Home Range Analyses

In the home-range study on Anegada, captured individuals were fitted with radiotransmitter belts (dog collars) with L and L Electronics (Mahomet, Illinois) two-stage transmitters and whip antennas affixed to them. I followed their movements using Merlin V receivers with collapsible hand-held yagi antennas (Wildlife Materials Inc., Carbondale, Illinois). Iguanas were telemetered from stations along 650 m of road during 1 mo periods in May 1988, May 1989, and March 1990. I also relied on monthly location checks, coupled with a close approach and sighting, until each animal's transmitter became weak or stopped transmitting. Animals were then recaptured in order to remove the radio gear.

Animal locations determined by angles between lines of position (LOP's) of $<30°$, or LOP's >10 minutes apart, were discarded as too inaccurate. Visual observations of study animals and burrow locations were recorded using differentially corrected code-based GPS (Pathfinder Basic Plus with Community Base Station, Trimble Navigation, Sunnyvale, California; accuracy ± 2 m). Home ranges were calculated from the combined data by the minimum convex polygon, 95% ellipse, and harmonic mean methods using TelemSS software (Coleman and Jones, 1988). Movement data were then transferred to a GIS database to relate the data to topographic features of the study site. Often, direct approaches were made to verify the radio-determined positional data. Attempts were made to locate as many burrows as possible by direct approach in morning or evening hours. Mass, snout–vent length (SVL), and sex were recorded prior to releasing animals at their respective capture sites.

Results

Residents that I interviewed reported that population density in all areas has decreased in their lifetimes (Fig. 1). Iguana distribution loosely conforms to the limestone regions of Anegada although the animals do inhabit adjacent sandy areas. Certain limestone areas in the central region of the island are not now and have not been, in the memory of residents, inhabited by iguanas. The principal areas occupied are along the north coast of the cay in a strip approximately one-third of the island's width. The extreme east and entire west ends have no iguanas. Exploratory surveys of the Citron Bush, Carey's (1975) study site, revealed no signs of iguanas there now. Populations also become more sparse along the south side; adults are rarely if ever seen there. The southern road on the western half of the island is sandy and readily shows tracks of crabs and small lizards crossing the sand. From 1988–1993, no tail drags or tracks of large iguanas were seen on this road during visits to Anegada, although I traveled it daily when on the island.

In contrast, juveniles up to a year old are quite frequently seen by locals on the southern third of the island's midsection, but after they reach approximately 20–25 cm SVL, the upper end of a stage Anegadians call "four o'clocks," they are no longer seen. The only two iguanas that I saw in the south were juveniles. Young are also dispersed throughout the population of adults to the north, particularly soon after hatching. During my study, I observed four juveniles <1 yr (two in October and two in March) and one larger subadult (≥ 1 yr old but <40 cm SVL; Carey, 1975; Goodyear and Lazell, 1994) in the Low Cay area. Two brief visits to Windberg Cay indicate that juvenile iguanas are, as first noted by Carey (1975), still regularly present there. Table 1 contrasts population density at the Bones Bight-Low Cay Study Site with that found in two other studies:

TABLE 1.—Population and sex-ratio results for three studies of *Cyclura pinguis* in the British Virgin Islands. M = male, F = female.

Study	Date	Location	Sampling area (ha)	Density (ha) (95% CI)	Sex ratio (M:F)
Anegada					
Carey	1968	Citron Bush	4.9	2.03	1:1
Mitchell	1988–1991	Bones Bight	42.6	0.36 (0.22–0.62)	2:1
Guana					
Goodyear and Lazell	1994	GIC environs	18.8	0.5 (0.35–0.69) or 0.7 (0.33–1.49)	1:3

Carey (1973) for Anegada, Goodyear and Lazell (1994) for Guana Island. I estimate that the total Anegada population currently consists of 164 individuals distributed over 9 km² of habitat on the 35-km² island.

Leaves of *Croton discolor*, an aromatic shrub in the Euphorbiaceae and dominant understory plant at the study site, were the most commonly eaten component in the diet of *C. pinguis* on Anegada. Next, they relied most heavily on the fruit of three species: *Byrsonima lucida* (Malpigiaceae) and *Coccoloba uvifera* (Polygonaceae), both soft and sweet when ripe, and *Elaeodendron xylocarpum* (Celastraceae), a bitter fruit with a thin dry rind of flesh surrounding a large pit. These three species were patchily distributed on the study site. *Dodonaea viscosa* (Sapindaceae) is a leathery-leaved shrub; its fruits are used as fish poison in some locales (Little et al., 1974). *Dodonaea* was an abundant understory plant on the study site and also grew as a tall (about 2 m) shrub. *Lantana involucrata* (Verbenaceae), another aromatic shrub, was also a common understory plant. Other items consumed each represented <1% of the diet and varied in availability dependent on distribution, fruiting season, and fruit production. Iguana skin was also present in feces when animals were shedding (Table 2).

TABLE 2.—Diet of rock iguanas on Anegada, British Virgin Islands. Relative bulk of incompletely digested items was analyzed for 27 fecal pellets and the contents of one stomach.

Items eaten	% of diet
Leaves	
Croton discolor	25.7
Dodonaea viscosa	5.5
Erithalis fruticosa	3.3
Lantana involucrata	2.1
Byrsonima lucida	0.8
Grass	0.4
Ernodea littoralis	0.2
Cordia rupicola	0.1
Solanum persicifolium	0.1
Subtotal	38.2
Fruit	
Byrsonima lucida	24.2
Coccoloba uvifera	13.9
Elaeodendron xylocarpum	5.7
Diegoia axillaris	4.9
Cordia krugii	3.3
Crossopetalum ilicifolium	0.3
Ziziphus rignonii	0.4
Acacia anegadensis	0.4
Subtotal	55.5
Animal material	
Invertebrates	0.9
Iguana skin	0.4
Subtotal	1.3
Unidentified material	5.1
Total	100

Home range estimates (Table 4) for the nine radiotagged individuals of *C. pinguis* were larger than reported for other West Indian iguanas (Carey, 1975; Iverson, 1979; Schwartz and Henderson, 1991) but were similar in size to those of animals previously tracked on Guana Island (Goodyear and Lazell, 1994). The home range of the female that was extensively tracked was smaller than the home ranges

Well fed individuals of *C. pinguis* on Guana Island had a mixed response to major components of the diet of iguanas from Anegada (Table 3). *Croton discolor* and *Dodonaea viscosa* were rejected entirely. Sugary fruits were taken immediately, and individuals would eat as many as offered.

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TABLE 3.—Responses to major components of Anegada rock iguana diet by iguanas on Guana Island. Number of iguanas tested (n) is shown.

Food item	Eaten	Not eaten	Tasted and rejected	n
Leaves				
Croton discolor		6		6
Dodonaea viscosa		4	1	5
Lantana involucrata		2	1	3
Byrsonima lucida	2			2
Fruits				
Coccoloba uvifera	5			5
Elaeodendron xylocarpum	1		5	6
Eugenia sp.	1			1

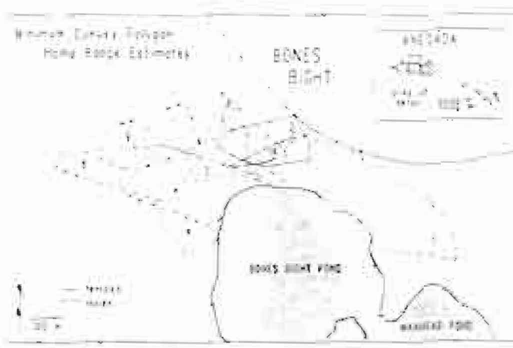


FIG. 2.—Minimum convex polygon home ranges of nine individuals of *Cyclura pinguis* on Anegada, British Virgin Islands.

of five males and larger than the home ranges of two males. The second female radiotracked had the smallest home range, but the size may have been underestimated because of a low number of telemetry fixes on this animal over a relatively short period of time (Rose, 1982). Minimum convex polygon home ranges of both sexes overlapped (Fig. 2), but 50% and 80% usage contours indicate that males avoid centers of activity of other males (Fig. 3).

Individuals frequently shared use of several burrows though simultaneous burrow use was not observed. Male 5 and female 2 used the same burrows on two occasions, and males 3 and 8 used two of the same burrows once each. The male with the largest home range used burrows occupied by three different females.

Of 14 adult iguanas captured in the Bones Bight-Low Cay study site, only five were female. Table 5 shows the SVL and body mass of individuals measured. The physical condition of the population appears to have degenerated since 1968. In all but one case, both males and females captured between 1988–1990 had proportionately lower body mass than males and females captured in 1968 (Fig. 4). In addition, the average SVL for both males and females collected during this study ($\bar{x}$ = 49 and 45 cm, respectively; Table 5) was low-

TABLE 4.—Home ranges of nine iguanas radiotracked on Anegada, British Virgin Islands. Estimates are in hectares; n = total number of radiotelemetry and GPS location fixes.

Iguana	Days tracked	Tracking period	Home range (ha): Minimum convex polygon	Home range (ha): 95% ellipse (nonparametric methods)	Home range (ha): 50% contour (harmonic mean)
Females:					
2 (n = 50)	31	May 1988–March 1991	2.8	2.6	0.1
14 (n = 8)	6	February 1990–May 1990	0.5	1.6	0.2
$\bar{x}$ females			1.7	2.1	0.3
Males:					
3 (n = 20)	24	May 1989–July 1990	1.9	7.3	1.7
4 (n = 22)	26	June 1988–March 1991	3.7	7.6	1.3
5 (n = 17)	12	May 1988–November 1989	4.4	2.4	0.7
6 (n = 36)	10	June 1988–January 1990	4.5	2.2	0.2
7 (n = 17)	11	May 1989–December 1989	9.0	18.5	1.5
8 (n = 11)	8	February 1990–June 1990	1.2	12.6	1.4
9 (n = 14)	10	February 1990–November 1990	3.6	6.7	0.5
$\bar{x}$ males			4.0	8.2	1.0
$\bar{x}$ both sexes			3.5	6.8	0.9

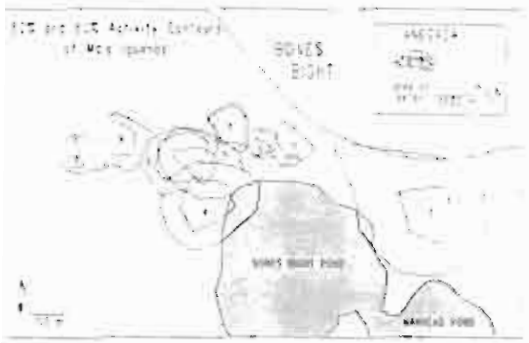


FIG. 3.—The 50% and 80% harmonic mean activity contours of seven males of *Cyclura pinguis* on Anegada, British Virgin Islands.

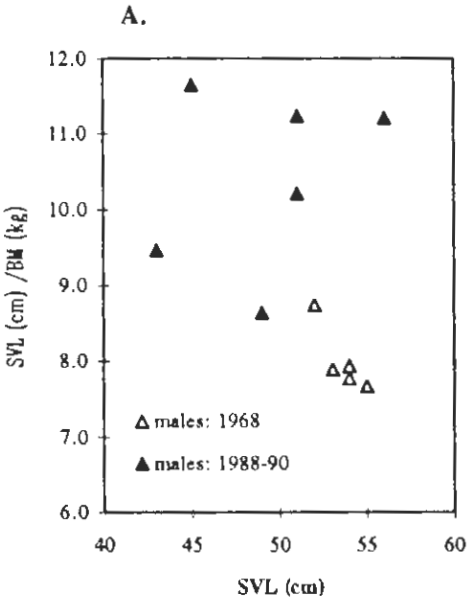
er than the average for males and females in 1968 ($\bar{x}$ = 53 and 47 cm, respectively: Carey, 1975).

DISCUSSION

It is my impression that the distribution of iguanas on Anegada has always been patchy and iguanas do not occur far from the limestone backbone of the cay. Iguanas can survive in sandy areas, however. Three study animals were never observed in limestone habitat; their home ranges included exclusively sand substrate. Also, certain limestone areas do not support, and have not historically supported, igua-

TABLE 3.—Snout-vent length (SVL) and body mass of iguanas captured on Anegada, British Virgin Islands. SVL measurements had an average error of ±3 cm depending on the position of the animals when measured.

Iguana	Length (cm)	Body mass (kg)
Females		
2	44	2.72
10	48	—
11	46	—
14	43	2.16
6 females	45	2.44
Males		
3	43	4.54
4	51	4.54
5	54	4.90
6	51	4.54
7	49	5.67
8	45	5.86
9	56	4.99
6 males	49	4.73



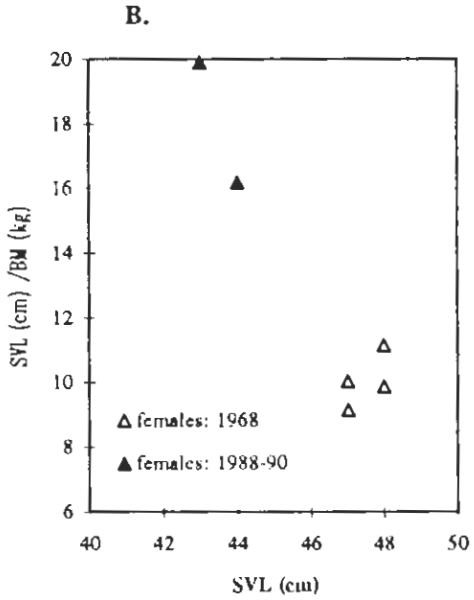


FIG. 4.—Snout-vent length (SVL)/body mass (BM) versus SVL as plotted for (A) males and (B) females of *Cyclura pinguis* captured in 1968 (Carey, 1975) and those captured between 1988 and 1990.

nas—notably the central area east of the salt ponds extending west to The Settlement. I believe this is due to the nature of the rock, which has been dissolved by rain to create a cement-like cap over much of the land. There is little soil and there are few trees.

Anegadians recognize that iguana abundance has decreased over the entire cay. Current quantitative density data from the Bones Bight-Low Cay area, compared with data from 1968 (Carey, 1973), show the same trend. I found densities of *C. pinguis* to be almost 10 times lower. Carey's study site in the Citron Bush seems to have no iguanas now; I found no evidence of them during walking surveys there. In the Citron Bush, disappearance of iguanas may be due partly to human predation and interference. Many former burrows had been filled in or covered with rocks. I also discovered several nylon monofilament nets encircling known burrow pits. Iguanas may have been captured and removed. As of 1993, it did not appear that iguanas had recolonized the area.

People living on Anegada consistently report that there is little predation of iguanas by humans. Anegadians do not eat them. Dogs and cats are said to kill iguanas, however. Goat-hunting dogs are notoriously indiscriminate, tackling either goats or iguanas when they flush them from shelter. Several feral dogs were also reported on Anegada in 1994. In the Bones Bight area, there were a large number of feral cats. I frequently saw their tracks and feces on the study site. These undoubtedly prey on young iguanas. Iverson (1978) documented that a population of 15,000 iguanas on Pine Cay, Caicos Islands, was "almost completely extirpated" over a 2-yr period by predatory dogs and cats.

The lack of recovery observed at Citron Bush reflects a low juvenile recruitment rate in general on Anegada. Carey (1973) commented on the unusual and perhaps unhealthy structure of the population, which consisted mostly of established adults. On Anegada as a whole, adult iguanas still are most frequently seen.

In the Bones Bight-Low Cay area, there has been little or no recent replacement of older animals by juvenile recruits since my study began. In general, hatchlings do not seem to survive past their first year, and subadults are rarely seen. This observation contrasts strongly with that for a population of *Cyclura carinata* on Little Water Key, Caicos Islands, where in the 1970's juveniles had a annual survivorship of 50% or greater during the first 6 yr of life (Iverson, 1979).

Over the entire cay, habitat quality has obviously declined since livestock was released two decades ago. Stock appear to eat all vegetation that can be reached that is not toxic or unpalatable. As a result, in most areas the dominant species are plants producing toxic or repellent secondary compounds. Of this group, *Croton discolor* is now the most prevalent understory plant in most regions of Anegada, as is typical for *Croton* in overgrazed areas (Little et al., 1974). *Croton astroites* and *C. rigidus* are dominant in the understory of overgrazed areas of other British and U.S. Virgin Islands (e.g., Guana, Necker, Tortola, Virgin Gorda, St. Thomas; and Hans Lollick, personal observation). In February 1993, I visited Little Goat Island, Jamaica, a locality from which *C. collei*, the Jamaican iguana, recently disappeared. Overgrazing by goats there promoted a dominant understory of another congener, *Croton linearis*.

Though *C. discolor* was listed as present in Carey's study, it had a low relative abundance of 8.8% and was not part of the iguanas' diet. Today *C. discolor* represents 30–70% of the understory in sections of Citron Bush, and it comprises >25% of the diet of *C. pinguis*.

In 1968, Carey found that 71% of the stomach contents was leaves; of this portion, 59% was composed of leaves avoided by livestock (*Reynosia*, *Cocoloba*, *Erithalis*, and to a lesser extent *Lantana*). Currently, diet on Anegada seems to have shifted. In my study, only 38% of the diet consisted of leaves; 95% of the leafy portion of the diet consisted of leaves avoided by feral livestock (*Croton discolor*, *Dodonaea viscosa*, *Erithalis fruticosa*, *Lantana involucrata*, *Bursonima lucida*, *Ernodea*

littoralis, *Cordia rupicola*, and *Solanum persicifolium*). Another 56% of the diet consisted of eight species of fruits, only one of which (*Cocoloba uvifera*, 16%) is eaten by stock. Thus, 73% of the fruit portion of the diet on Anegada does not overlap with that of the free-ranging livestock.

Auffenberg (1982) listed common native plants occurring in the habitat and diet of *C. carinata* on Pine Cay, Caicos Islands. While he did not mention that any species of *Croton* occurs there, *Dodonaea viscosa* and *Lantana involucrata* are common. Neither of these plants was eaten by the iguanas, though 47 other plant species were part of the diet. Two of the plants that together comprise 41% of the diet of *C. pinguis*, *Byrsonima lucida* (= *B. cuneata*: Little and Wadsworth, 1964) and *Cocoloba uvifera*, were common on Pine Cay, but together constituted only 3% of the diet of *C. carinata*.

Cyclura carinata was reported to eat some plants with toxic secondary compounds, notably *Metopium* (poisonwood) and *Hippomane* (manchineel), neither of which occurred in the Bones Bight-Low Cay study site on Anegada. Auffenberg (1982) noted that less poisonous parts (fruits) were more commonly eaten and that *C. carinata* was probably "forced to eat small amounts of a variety of foods in order to maintain a wide secondary compound detoxification potential." If, as Iverson (1979) suggested, the dense population of *C. carinata* at Pine Cay was food-limited, Auffenberg reasoned that it would be advantageous for iguanas to retain the ability to digest the widest diversity of food species. I believe that, in the case of *C. pinguis*, the ability to exploit foods containing potentially toxic secondary compounds that mammalian herbivores cannot tolerate has probably been the iguana's salvation to date. Toxic or repellent plants comprise most or all of its leafy diet.

The total percentage of "unidentified" material in feces that I examined (5%) was less than Carey found (14%), indicating that most of the material eaten was essentially intact in the feces, and reflected the diet with reasonable accuracy. The unidentified 5% that I found may have included the highly digestible food items that the animals encountered. Proportional volumes of invertebrate consumption are probably not comparable between fecal material and stomach contents; not much is left of soft-bodied invertebrates once they have passed though the digestive tract. The difference may also involve the species eaten. The current selection of food plants seems to be less digestible and may be less nutritious. This conclusion was supported by my inability to analyze scats from iguanas on Guana Island living within the sheep exclosure. Food items there were well digested and often not recognizable. Iguanas that do not compete with livestock for food seem better able to digest items that they select to eat.

Feeding experiments revealed that iguanas on Guana Island refused to eat several principle items in the diet of iguanas on Anegada. None of the leafy species was consumed. This lends support to the notion that the diet on Anegada is one of necessity, not preference. Further, studies of iguana distribution and abundance on Guana resulted in the conclusion that habitat outside the sheep exclosure was of low quality (Goodyear and Lazell, 1994).

Along with a decline in population and a change in diet since 1968, social organization now differs as well. From the data available, it appears that home-range size and spacing on Anegada differ from that documented by Carey (1975): home ranges in the Bones Bight-Low Cay area average 100 times larger, and either abut or overlap.

The sex ratio for iguanas on Anegada now differs dramatically from the 1:1 observed by Carey in 1968. He substantiated that high female to male ratios are the norm for adult lizards. Since 1968, the ratio has shifted in the opposite direction, however. Males on Anegada are now twice as abundant as females. Anecdotal evidence suggests that females do not thrive on Anegada. I recaptured female 2 five times over a 3-yr period and measured changes over a 9-mo period. This animal never gained mass over the course of the study, though two males did grow. On Guana Island, within the sheep exclosure,

one female grew from a hatchling to the size of female 2 on Anegada between 1991–1993. Two other iguanas on Guana Island, first encountered in 1991 when they were about the same size as female 2 on Anegada, are now at least one-third larger (personal observation).

Females may have more difficulty than males in meeting their energy requirements in areas with degraded habitat. Each year, females must invest considerable energy in producing large clutches of eggs. This extra cost may deplete female fat stores, decrease general fitness (resistance to disease, parasites, and stress), and consequently increase female mortality relative to males. Carey felt the that the 1:1 sex ratio, combined with the spacing behavior that he observed (home ranges of male-female "pairs" overlapped each other but not those of other animals), indicated that *C. pinguis* was facultatively monogamous. In dense iguana populations, polygamy is common (Iverson, 1979; Schwartz and Henderson, 1991). In my study on Anegada, "pairs" were no longer definable. With the present imbalance in sexes, a monogamous system would depend on the celibacy of one-half of the male population, which is not a viable reproductive strategy.

Carey's work was conducted during the mating season, and the small home ranges that he observed were probably partly attributable to males guarding females. Conversely, the large home ranges of males observed in my study might have been related to unpaired or subdominant males "cruising" for females. The two males likely to have mating opportunities in this study had the smallest home ranges and stayed close to or shepherded females.

The overall changes in home range size observed for *C. pinguis* may have been caused by several factors. Some of the differences are due to methodology. Carey's study lasted only 40 days, and animals may not have used all of the area encompassed by their home ranges during that time. Most of the animals in my study demonstrated wide movements within several days of capture and tagging, however. I suspect that degraded habitat quality and resultant low population density and imbalanced sex ratio on Anegada have led to the extensive changes in social organization observed. Decreased iguana density might allow expansion of home range size, but expansion might also be advantageous if it were to increase foraging opportunities in habitat with sparsely distributed resources. The decreased number of females relative to males on Anegada may apply additional pressures on unpaired males to venture farther than was either necessary or prudent when each had a mate.

In concert, the population decline of *C. pinguis*, dietary shifts, changes in home-range size and spacing, social relationships, sex ratio, and physical condition reflect a severely stressed and endangered population. Including Guana Island's estimated population of 20 adults bred from eight relocated individuals (Goodyear and Lazell, 1994), conservatively, the total population of *Cyclura pinguis* contains <200 individuals. The government of the British Virgin Islands is considering a plan to establish a National Park on Anegada to protect and restore the iguana population and associated biotic communities. Critical first steps are the construction of a stock-excluding fence surrounding areas containing the largest subpopulations of iguanas, elimination of grazing stock from the enclosure, and restoration of diverse native plant communities.

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Along with supporters of this work I thank my partners at the National Parks Trust, R. DeRevariere, J. Banks, J. Blaine-Seal, O. Shirley, and R. Norton. I am very grateful to those who assisted in the field: R. and V. Smith, S. Avvazian, N. Feller, J. Randell, K. Johnson, and V. Vanderpool. I appreciate the experience and help of longtime island residents Captain I. Smith, A. Lewins, E. "Bruser" Norman, H. Vanterpool, G. V. Smith, C. Faulkner, Sr., and M. Soars, who pored over plant samples or discussed stock diets and iguana distributions with me. I thank S. Wheatly for her boundless enthusiasm, L. Wheatly for timely

advice, and both for their friendship and hospitality. C. Krebs examined my data and helped me select an appropriate home-range estimator. G. Proctor and J. Smith very kindly identified herbarium specimens that I collected on Anegada. I thank G. Gerber, J. Lazell, C. R. Sheep, and one anonymous reviewer, who critiqued the manuscript. For help throughout, I thank my husband G. Mitchell who is always ready for the best and worst and calls it all adventure.

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2300 STEELE STREET DENVER, CO 80205-4899 PHONE (303) 331-4100 FAX (303) 331-4125 TDD (303) 370-8093

January 16, 1998

Dr. Numi Mitchell
The Conservation Agency
67 Howland Avenue
Jamestown, RI 02835

Dear Dr. Numi Mitchell:

Happy New Year! We are writing to request your assistance in putting together a reference text tentatively titled "*Endangered Animals: Conflicting Issues*." The book will include 50 *short* case studies on a wide variety of endangered species from throughout the world. As the title suggests, the book will focus on conflicts surrounding efforts to conserve species. Chapters will therefore focus on primarily non-biological issues (although some biology and ecology will be covered). In addition, since the volume will serve as a reference text, we are requesting a minimum number of references (which should be no problem for most species, but we can make exceptions). We will edit the volume, which will be published by Greenwood Press. Proceeds from sales (editors' share) will support conservation activities of the Denver Zoo's Department of Conservation Biology.

We are requesting your assistance because of your expertise in the recovery efforts for Anegada Iguana (*Cyclura pinguis*), as well as the quality of your past work. The publisher has requested that the reading level be kept relatively simple (approximately a *New York Times* level). We believe the chapters, being relatively short and written at a fairly simple level, should take relatively little time to complete.

We developed an outline for the chapters, which is enclosed. The total length of each chapter cannot exceed about 2,400 words (approximately 8 double-spaced pages). This includes references. If there are several conflicts surrounding conservation efforts, you may wish to focus on just one or two. We have set a July 1, 1998 deadline for the first draft of the chapters. We believe this should pose no problem, as you should be able to write your chapter rather quickly. Finally, we would like to include photographs of as many species as possible and request that your chapter be accompanied by a high quality photograph.

Denver Zoo 1896-1996

AZA

If you would like to contribute an additional chapter, please contact us as soon as possible, as we only have space for 50 case studies and contributors will be selected on a first come basis (we are contacting over 50 possible contributors, as undoubtedly some people will not have the time or desire to contribute). Also let us know if you would like to contribute a chapter for a species other than the one for which we contacted you.

Finally, if you agree to contribute, please give us up-to-date, complete contact information for you over the next 12 months. We would prefer to communicate via e-mail, if possible. Please get back to us as soon as possible. We hope you are willing to contribute to this volume and look forward to working with you.

With best regards,

Rich Reading, Ph.D.
Conservation Biology Director
(303) 376-4945
zooresearch@denverzoo.org

Brian Miller, Ph.D.
Conservation Biology Coordinator
(303) 376-4944
zooconservation@denverzoo.org

Word count: 2706

Common Name: Anegada Iguana

Scientific Name: *Cyclura pinguis*

Order: Sauria **Family:** Iguanidae

Status: CITES: Appendix I; IUCN: Critically Endangered; not listed or protected inside the BVI

Threats: Dog and cat predation, competition from feral livestock, habitat degradation and loss, and poaching.

Habitat: Dry tropical forest, and scrub, seasonally found in coastal strand, occasionally found in salt marsh or salt pond environs.

Distribution: Currently found on Anegada, Guana, and Necker Islands, British Virgin Islands. Formerly widespread on the Puerto Rico Bank (Pregill 1981).

Description: The Anegada rock iguana (*Cyclura pinguis)* is a relatively large and stout member of its genus. Males have been recorded with snout-vent lengths of 56 cm and may grow larger. These iguanas have dusty brown backs which can be vertically barred with black. Their legs, sides, and dorsal spines are often a brilliant turquoise blue. Commonly, the dorsal spines are quite small, especially on females. Juveniles are most colorful, patterned with a series of black chevrons crossing their green or blue-green dorsal surfaces. When Anegada iguanas are agitated their eyes flush bright crimson.

Natural History: The range of *Cyclura pinguis* was reduced to Anegada when the Virgin Islands became densely settled. Anegada is made of old, reef-tract limestone and sand. The island is honeycombed with holes, caves, and other rocky shelter sites -- ideal living quarters, or escape retreats, for iguanas. Anegada's human population has always been relatively low and there are few dogs and cats, and to date, no mongooses. Jointly these qualities made Anegada the last reasonably safe environment for *C. pinguis*. On Anegada, iguana distribution remains closely tied to the more porous limestone habitats, though they use adjacent sandy areas for burrowing and nesting as well.

Both Guana and Necker are largely volcanic in origin and have few naturally-occurring shelter sites. The iguanas must dig their own burrows. As a result, on these cays, fewer burrows are used and animals are more arboreal. Iguanas are much more vulnerable on these privately-owned islands, but non-native predators such as cats and dogs are either controlled or are not permitted there.

C. pinguis is predominantly herbivorous. Invertebrates such as centipedes (*Scolopendra*), larvae of a moth (*Pseudosphinx tetrio*), and scarabid beetles are also eaten. Iguanas rely heavily on fruit in season. On Anegada, where the iguana's distribution entirely overlaps with feral ungulates, the diet consists mostly of plants that are not favored by livestock; many containing secondary compounds. One such plant, *Croton discolor*, has dramatically increased in abundance since livestock were released on the cay in the late 1960's. *C. discolor* was found recently to comprise one-third of the iguana's diet on Anegada (Mitchell 1999). The flora of Guana is quite different. Iguanas tend to inhabit areas where sheep do not graze. Native plants eaten on Guana include large quantities of *Centrosema virginiana* (a tender-leaved pea), flowers of *Tabebuia heterophylla*, seed pods of *Capparis cynophallophora*, and leaves of *Stigmophyllon emarginatum* and *Capparis flexuosa*.

Guana and Necker Islands have low quality iguana forage in most areas. Both of these islands have been affected by feral sheep, goats, and possibly other grazing ungulates. As with Anegada, the vegetation has shifted in composition to plants rich in secondary compounds that are either distasteful or toxic to livestock. Guana still has feral sheep and goats though efforts are being made to reduce or eliminate them. Necker's livestock has been removed, but vegetation still resembles that of islands on which livestock grazing occurs.

Along with a decline in population and a change in diet since livestock release in 1968, social organization now differs as well. In 1968 the average home range size for iguanas on Anegada was less than 0.1 ha and male home ranges had free space between them. The sex ratio was 1 male: 1 female. Males and females appeared to be monogamous and lived in separate, but closely adjacent burrows (Carey 1975). By 1988, home range size and spacing appeared to differ in two ways: 1) home-range size averaged 100 times larger, and 2) male home ranges abutted and overlapped slightly (Mitchell 1997, 1999). The number of females declined: the sex ratio was 2

males : 1 female. "Pairs" were no longer clearly definable because several males would enter the home range of the few females present. Males suspected of having a mate had a principal burrow near that of a female, used some of the same burrows as the female, and had noticeably smaller home ranges -- presumably to guard the female against wandering batchelors (Mitchell 1999).

Females lay 12-16 eggs between May and June. Females inhabiting sandy areas nest in their principal burrows or in the dunes; those in rocky areas travel to find a spot in which to dig. On Anegada, some females may swim to Winberg Cay, a tiny islet in Red Pond, to nest. On Guana island, iguanas nest in seagrape-dominated beach strand. Clutches hatch in the late summer (August-September) as the fall rainy season commences the vegetation becomes more lush. If conditions are favorable, hatchlings can mature to reproductive size (about 450 mm snout-vent length, Carey 1975) in three to four years.

Conflicting issues:

Context: Anegada is no longer a safe refuge for iguanas. Since the late 1960's iguanas on Anegada have experienced a massive population decline: their density in what used to be considered good habitat is almost ten times lower than former levels. The drop in numbers is probably due to a number of causes: 1) feral dogs (first reported in 1994) which are known to kill adult iguanas, 2) an exploding population of feral cats which prey on juvenile and subadult iguanas, 3) human poachers trafficking exotic pets, and 4) feral livestock. Feral livestock represent Anegada's biggest drawback -- the island teems with sheep, goats, donkeys, and cattle that cyclically breed to carrying capacity then starve after stripping the landscape of all palatable vegetation. These ungulates compete with the iguanas for food. As a result, the iguana's diet has shifted; to plant species that livestock do not eat, mostly those with secondary compounds. Many of these plants are poorly digested and therefore of dubious nutritional value.

Attempts have been made to restore iguanas to parts of their former range. Between 1984-6, eight iguanas from Anegada were relocated to Guana. In vegetatively diverse regions of Guana these individuals and their descendants are thriving and reproducing (Goodyear and Lazell 1994); and some of the offspring have been relocated to Necker Island.

Prior to the 1960's, the residents of Anegada -- descendants of former slaves and pirates -- relied on a combination of farming, animal husbandry, and fishing for their livelihoods. The island was neatly and effectively partitioned by a system of stone walls, painstakingly constructed by residents, that retained livestock, fenced agricultural crops, and defined ownership.

Residents maintain that ownership of the land was granted to them by Queen Victoria. In an 1885 ordinance pertaining to Anegada, the Crown agreed to grant land *with the proviso* that landowners have their property boundaries surveyed. Not one Anegadian did so (Renwick 1987). In 1961, under new legislation, the "Anegada Ordinance," the British Crown assumed administration of most of the island and, along with the Government of the BVI, leased all but 607 ha to a Canadian development firm in 1968. The company, Development Corporation of Anegada, Ltd., began to develop the cay by bulldozing the network of stone walls. The stock animals (goats, sheep, cattle, burros, and swine) escaped to the bush and began to freely range the cay.

In combination with a prolonged drought, crops were raided and failed. Anegadians turned to the sea for a living. The livestock release was also a turning point for iguanas who now had mammailian herbivores as competitors. Ironically, the development firm soon folded, abandoning warehouses, rock crushers, and excavating equipment. Some Anegadians take credit for driving the firm off the cay. Shortly afterward, the government began a reassessment of land claims on Anegada and some titles were granted to residents (Lands Adjudication Act, 1970).

The idea of creating a National Park on Anegada was endorsed by the BVI Executive Council in 1981, and proposed in 1986 in the BVI "System Plan" (Geoghegan et al. 1986). In 1987 the Governor appoined a one-man commission who recommended an equitable division of lands on Anegada (Renwick 1987). A respected group of community leaders formed the "Anegada Lands Committee" to mediate and settle remaining land-ownership issues. In March 1993, they approved the Anegada National Park concept in principle.

Based on iguana survey work (Mitchell, 1999), a joint proposal from the National Parks Trust and The Conservation Agency was submitted to the Town and Country Planning Department that recommended establishment of three terrestrial conservation zones on Anegada (Goodyear and DeRavariere 1993). These regions did not include any lands for which titles were already held.

Town and Country Planning was at that time producing the "Anegada Development Plan"(Government of the British Virgin Islands 1993), in which the conservation zones recommended were closely adopted. In November 1993, the Development Plan document was released to the public. With their land claims still unresolved, the maps enraged residents preventing dialog when the Chief Planner arrived to formally introduce the plan. To date, disagreements are still rampant and consensus on ownership and property boundaries remains elusive. Therefore, the Anegada Development Plan, and the National Park proposal, have been tabled at present.

The residents of Anegada will not set aside land for the iguana until they have land for themselves. In fact, the current prevailing sentiment on Anegada is to disallow or discourage help of any kind for the iguana until the government has given Anegadians titles to their land.

Conflicting Issues: Several problems impede establishment of a National Park, or some form of sanctuary, to protect the Anegada iguana: First, who is entitled to claim land on Anegada: a) everyone born on Anegada and their descendants (there are a number of former Anegadians, and first or second generation offspring, currently living in New York, USA who have submitted claims for land), b) only those born on Anegada, c) only those born and raised on Anegada, or d) only those born, raised, and still living on Anegada? Second, should the iguana be granted land before the people's claims are settled? Third, Who should decide whether the iguana gets a land allocation and who chooses which land: a) the British Crown (appointed official), b) the BVI government (locally elected officials), c) the citizens of Anegada (but see the first issue), or d) some combination of a, b, and c? Although there are only about 150 residents, Anegadians have swayed both elections and elected officials in the past. Elected BVI officials will not allocate land for iguanas because it would widely displease voters on Anegada.

Complicating these issues is the fact that the general community on Anegada has not be shown how or why a National Park would benefit them. The potential benefits of ecotourism should be explained to generate enthusiasm and local support. In addition, although the National Park Trust is ostensibly supporting establishment of a National Park on Anegada it is rendered ineffective because, as a branch of the BVI Government, ultimately, it gets its directive from the

politicians. Finally, because of past interactions with the Crown and government officials, Anegadians are skeptical and suspicious of outsiders. They do not believe anyone has their best interests at heart.

Prognosis and Recommendations: From the conservation standpoint, the first order of business on Anegada is to set aside land for the iguana, fence it, and remove livestock. It will probably be necessary to assist the recovery of native plant communities that provide forage for iguanas. Experiments are currently underway to determine whether livestock exclusion is sufficient to promote recovery of diverse native plant communities (a passive effort) or whether active replanting or soil enrichment is required. Conditions on Necker suggest that active management will be necessary, as the cay retains a depauperate plant community ten years after livestock removal.

Getting a land allocation for iguanas may be more difficult than managing it. To get approval for an iguana sanctuary the government should attempt to satisfy the concerns of residents first. The government should set a target date for settling all private claims to land titles on Anegada. If agreements cannot be reached by this deadline it is of paramount importance that the Crown assume responsibility for *C. pinguis* and, as holder of the land granting privilege, as well as the lands proposed for the National Park, set aside a protected area for iguanas. No residents currently on Anegada lay claim to areas in the proposed National Park, except as historical grazing range. Most of the area is lowland or wetland and not buildable.

The Anegada Development Plan (Government of the British Virgin Islands 1993) did not discuss management strategies for proposed conservation zones. Some suggestions for park development and use follow:

A national park should be established and managed to promote recovery and proliferation of the island's rare, indigenous, and endemic species, particularly the iguana. Focus should be on restoring and repairing native habitats that have been damaged by overgrazing. The area should be fenced. Nature trails and boardwalks could be developed, but buildings (except shade shelters and observation platforms) should not be permitted. The park should be staffed with Anegadian wardens and interpretive personnel. Fishing and salt collection in ponds could continue in

accordance with BVI regulations, but must not interfere with the reproduction or foraging habits of native animals.

Conservation areas should be left unfenced, but should not be developed. Some eastern regions contain important habitat for relict subpopulations of iguanas and waterfowl. Spectacular, large native trees persist to the east and on the west end there is sandy nesting habitat for iguanas living in limestone areas adjacent. Nature trails might be considered.

Coastal Reservation should be managed for iguanas that nest behind dune ridges or in coastal strand communities and sea turtles that nest in sandy seaward regions. Clearing vegetation and foot traffic in the dunes should be avoided and buildings (except shade shelters) should not be permitted to avoid disruption of nesting sites. The beaches should be left in their pristine condition to promote continued recharging of the turtle population. Turtling, now legal, should be discontinued entirely. Designation of the Coastal Reservation as public domain would ensure that Anegada retains its trademark vast white beaches that provide a magnet for visitors to the BVI.

The advantage of setting these lands aside must be properly explained to the Anegadians. Establishment would benefit iguanas and Anegadians alike. The iguanas would benefit from management policies designed to promote their recovery, while for Anegadians, the park could provide economic benefits to the community in the form of jobs and business expansion. Within the park, positions could include interpretive naturalists and guides, wardens, maintenance personnel, park restoration staff, and construction workers. Outside the park there would be increased demand for service-oriented businesses, such as grocery stores, restaurants, bars, gift shops, dive businesses, rental shops, bed and breakfast, hotel facilities, and taxis. Other benefits could include government job training and development of a museum associated with the park to showcase both natural history and historical features of Anegada (Goodyear and DeRavariere 1993).

It takes capital to develop attractive tourist destinations. Anegadians should quickly gain assistance (such as development grants) from the world conservation community to develop a park that they can staff and run if they chose to conserve iguanas and their habitat. This would make

Anegada the only British Virgin Island where profits could be made largely by locals as opposed to outside investors.

In 1997 the National Parks Trust began a headstart program for hatchlings on Anegada (raising iguanas for several years before release to the wild) and planning a feral cat removal program, valuable steps to reduce predation pressures on young iguanas. Given the current condition of the habitat, however, it is unlikely that many headstarted individuals released, or wild juveniles, will survive to maturity in the bush unless this effort is coupled with creation of a livestock-free managed area which can sustain higher numbers of adults. It is urgent that decisions to allocate and manage land for iguanas are made rapidly. Without action, the iguanas on Anegada may be extirpated within the next decade.

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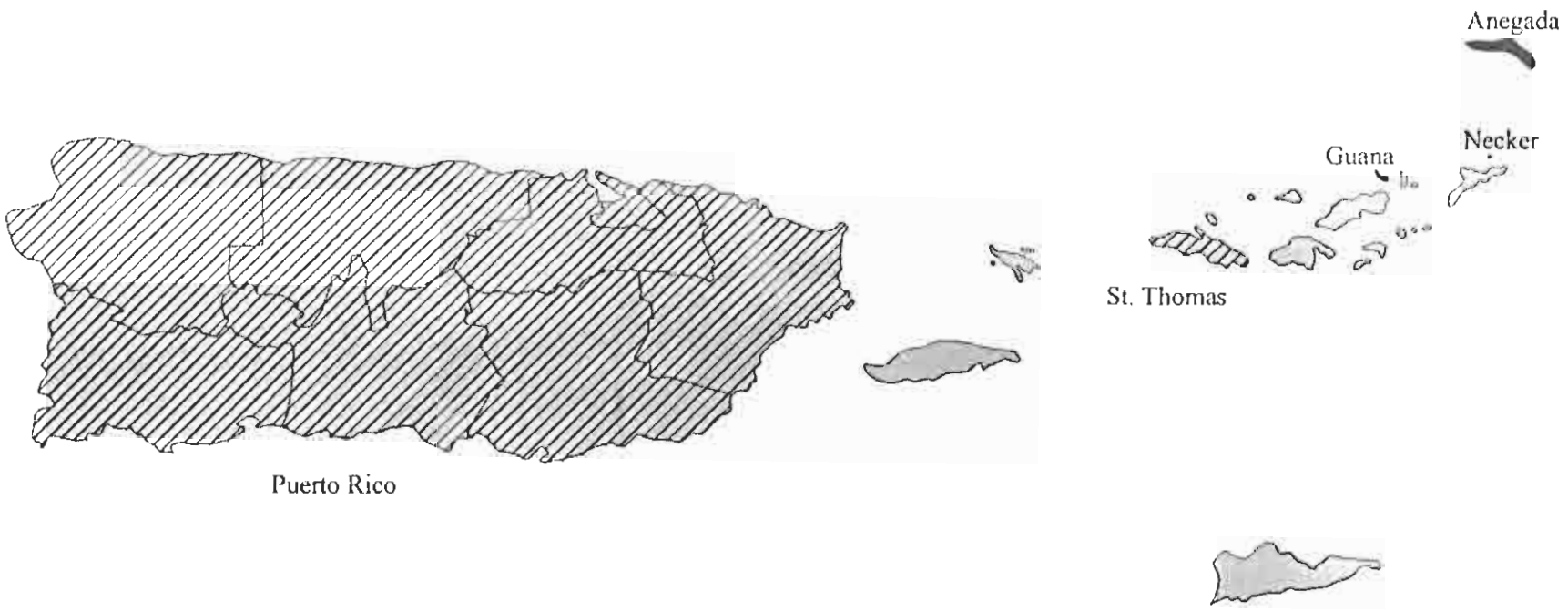
Past and present distribution of *Cyclura pinguis* on the Puerto Rico Bank



Subj: **RE: Anegada Report**
Date: 04/13/1999 4:55:27 PM Eastern Daylight Time
From: numi@wsii.com (Numi Mitchell)
Reply-to: numi@wsii.com (numi@wsii.com)
To: dveitch@kiwilink.co.nz ('Dick Veitch')
CC: orgcurherps@denverzoo.org ('Rick Haeffner'), jcinjtown@aol.com ('Skip Lazell')

Dear Dick:

Thanks so much for your response. I enjoyed your Anegada report very much and hope they get on with your recommendations quickly. What a sad and, as you say, "classic" story. As you know I agree with you that the livestock is the biggest threat to iguanas there. The cat population has really skyrocketed since the development of the dump, however, and they are a much bigger problem to juveniles then they were when I was there. In the TCI the iguanas are much smaller and even adults are threatened by cat predation (especially the females which are tiny compared to those on Anegada).

Regarding my problem in the TCI your report was extremely specific and helpful. I look forward to seeing your other papers. For the Anegada report most of the figures didn't come through on the word document. I think, however, the only necessary one would be Figure 2 from Appendix I (the cat bait station). If you had a chance to fax or mail it to me I would be grateful.

1080 sounds like scary stuff but the best stuff, supplemented by trapping as you recommend. Without seeing your designs I have been thinking of fabric Quonset huts for bait stations that cover/hide the poison bait from birds and protect from rain. If you can visualize 2 pieces of wire or fiberglass bent in a hairpin shape (with a hairpin turn about a foot wide - a little wider and higher than a croquet wicket - but plugged into the ground the same way). These two wires will be at either end of a 2' X 2' square of rip-stop nylon that has the ends sewed to make tubes that the wires slide through. Is that clear? We have a half-round nylon Quonset hut tent - kind of a tunnel - that will allow a cat to comfortably pass through. We put these regularly along the sandy side of the island and especially on cat trails. I was thinking the bait could be a 1080 injected frozen mouse but I am leaning towards a ball of smelly cat food (maybe laced with catnip?) then definitely laced with 1080. How would this compare with the bait commercially produced that you mentioned in the Anegada report? If we used bait "balls" we could make these up in advance and freeze the balls and go over with zip locks full and put a ball under each tent. One of the appealing things about this is also that if we do this in the sand we can brush the area free of tracks daily and get some idea of bait station visitation. The advantage I imagine of the Quonset hut is that the nylon tents can be made in advance and, laid flat, will pack to nothing. We can get wire down there or bring it. What do you think?

Thank you for your reminder to consider cat diet. I think they must rely on rats, mice, small lizards, and seabirds during nesting season. You have made me sure we shouldn't attempt a poisoning campaign during the seabird nesting season because the cats will surely have all the food they need at that point. Otherwise the food supply is probably relatively stable at low levels.

On the other topic. I would really enjoy meeting you. It would be great to be able to meet you down there but at this point we are in the early stages of scraping together a (rather skimpy) budget. I am not sure of my summer schedule yet (which depends on others) but assuming we aren't committed elsewhere we would love to see you if you want to deviate your trip to Jamestown after 30 May. We can put you up and give you plenty of local food and drink if you can get yourself to Providence. I know Skip would like to meet you and he lives close-by - but he may be in Hong Kong at that time. We could talk about this more as our summer (and your winter) plans become solidified.

Glad to make this connection! Best wishes, Numi

Numi C. Mitchell, Ph.D
The Conservation Agency, Branch Office

---Original Message---
From: Dick Veitch [SMTP:dveitch@kiwilink.co.nz]
Sent: Tuesday, April 13, 1999 8:02 AM
To: numi@wsii.com
Cc: orgcurherps@denverzoo.org
Subject: Anegada Report

<< File: Anegada Report.doc >> << File: ATT00000.txt >> You are most welcome. And you may well recognise passages about Anegada that were taken from your writing - probably a draft of your published paper. If I remember correctly, my thoughts at the time were that they should have taken more note of your report. Cats are less of a problem than
the loss of iguana food caused by browsing animals. I would certainly appreciate a printed copy of your paper - see my snailmail address below.

I will post copies of the few cat papers I have but, truth is, we do more than we write.

I am not keen on giving you too much guidance on cat eradication without seeing the island beyond saying that I would not depend on a single method to remove the cats. What is the diet of the cats? What are the seasonal fluctuations of that diet? I find that I do need to see these places and see all the other things that are, or are not, present before giving advice
beyond the things that I have written already. Anegada was a classic as you
will read.

Now, to be helpful. I will be flying over that part of the world in late May and would love to stop off and meet with you. By "that part of the

world" I mean a bit of USA. I will be flying to Galapagos on 24 May for a meeting which currently has me leaving Quito to head north on 30 May. I could divert to meet with you some place. My present route is Quito, San Jose (Guatemala), Los Angeles. Ideally I would love to visit your island. My time would be free but you would need to cover all expenses.

ANOLIS CRISTATELLUS WILEYAE (Virgin Islands Crested Anole). **HERBIVORY.** On Guana Island, British Virgin Islands, at 0730 h on October 1997, we watched an adult female crested anole chewing and swallowing the bright yellow flower of *Tecoma stans*, a naturalized ornamental shrub native to Central America as far north as Texas. Lazell and Perry (Herpetol. Rev. 1997. 28:150) report frugivory in this species, but were misinformed about one plant that we reported the anoles to be eating, *Trichostigma octandra*. We take this opportunity to correct that identification to *Rivina humila* (Phytolaccaceae), "blood berry."

We are indebted to Dr. George Proctor for redetermining this species from a patch the anoles were eating in 1996. They were eating its berries from the same patch in 1997.

Submitted by **JAMES LAZELL** and **NUMI C. MITCHELL**, The Conservation Agency, 6 Swinburne St., Jamestown, Rhode Island 02835, USA.

Whittier College
13406 Philadelphia Street
P.O. Box 634
Whittier, California 90608

(310) 907-4200
Fax (310) 698-4067

Department of Biology

19 February 1999

Dr. James D. Lazell
The Conservation Agency
6 Swinburne Street
Jamestown RI 02835

Dear Dr. Lazell:

Thank you very much for your interest in our paper on helminths from the British Virgin Islands. My reprint supply on this paper is dwindling so I am sending you 12 plus 100 photocopies of it. I hope this will meet your needs. It is too late to order more. If only I had known, I would have ordered 100 extra reprints for you.

Might you know of any places where other herp. samples from your research efforts are deposited other than the MCZ? The collections manager there ignored my loan inquiry a few years ago, so I gathered MCZ was off limits for parasite investigations. Sometimes herpetologists have forgotten collections sitting in corners of laboratories. We have made good use of these in the past, particularly in our study of Anolis acutus using material Rodolfo Ruibal collected and our work on Sceloporus malachiticus from Costa Rica using material from Ken Marion. After our investigation we deposited the specimens in the herpetology collection of the Natural History Museum of Los Angeles County. Might you know of any such collections? Copies of these papers and our other works on Anolis lizards and Caribbean frogs are enclosed.

Again, many thanks for your interest in our work. I would greatly appreciate hearing any of your ideas for obtaining additional specimens (reptiles or amphibians) for future parasite studies.

Sincerely yours,

Stephen R. Goldberg

Stephen R. Goldberg
Professor of Biology
sgoldberg@whittier.edu

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65(2), 1998 p. 259–262

Research Note

Helminths of the Lizard *Anolis cristatellus* (Polychrotidae) from the British Virgin Islands, West Indies

STEPHEN R. GOLDBERG,[1] CHARLES R. BURSEY,[2] AND HAY CHEAM[1]

[1] Department of Biology, Whittier College, Whittier, California 90608 (e-mail: sgoldberg@whittier.edu) and
[2] Department of Biology, Pennsylvania State University, Shenango Campus, 147 Shenango Campus, Sharon, Pennsylvania 16146 (e-mail: cxb13@psuvm.psu.edu)

ABSTRACT: Sixty-two *Anolis cristatellus* from 7 islands of the British Virgin Islands were examined for helminths. One species of trematode, *Mesocoelium monas*, 1 species of cestode, *Oochoristica maccoyi*, 6 species of nematodes, *Parapharyngodon cubensis*, *Spauligodon anolis*, *Trichospirura teixeirai*, *Physaloptera* sp. (larva), *Porrocaecum* sp. (larvae), and *Rhabdias* sp., and 2 species of acanthocephalans, *Centrorhynchus* sp. (cystacanths) and unidentified oligacanthorhynchid cystacanths, were found. *Anolis cristatellus* represents a new host record for *O. maccoyi*, *T. teixeirai*, *Physaloptera* sp., *Porrocaecum* sp., and oligacanthorhynchid cystacanths.

KEY WORDS: *Anolis cristatellus*, Polychrotidae, helminths, British Virgin Islands.

Anolis cristatellus Duméril and Bibron, 1837, occurs in Puerto Rico and its offshore islands and the U.S. and British Virgin Islands and has been introduced into the eastern Dominican Republic and southeast Florida (Schwartz and Henderson, 1991). The only reports of helminths have been from populations of *A. cristatellus* from Puerto Rico (Chitwood, 1934; Cofresí-Sala, 1964; García-Díaz, 1966; Bain and Chaniotis, 1975; Acholonu, 1976). The purpose of this note is to report helminths of *A. cristatellus* from the British Virgin Islands.

Sixty-two *A. cristatellus* from the British Virgin Islands were borrowed from the Texas Memorial Museum, University of Texas–Austin (TNHC) and examined for helminths: accession nos. TNHC 55696–55707, 55762–55781, 55808–55809, 55814–55824, and 55831–55847. Lizards were collected by hand-held noose in 1993 and 1995, preserved in 10% formalin, and stored in ethanol. They were from 7 islands: Anegada Island (N = 6, mean ± SD snout–vent length [SVL] = 55.8 ± 8.6 mm, range = 47–68 mm), Beef Island (N = 8, SVL = 63.9 ± 4.6 mm, range = 56–68 mm), Guana Island (N = 3, SVL = 58.0 ± 3.6 mm, range = 55–62 mm), Necker Island (N = 12, SVL = 66.3 ± 2.5 mm, range = 61–70 mm), Norman Island (N = 12, SVL = 59.9 ± 4.6 mm, range = 51–68 mm), Tortola Island (N = 11, SVL = 60.8 ± 2.0 mm, range = 57–64 mm), Virgin Gorda Island (N = 10, SVL = 54.2 ± 3.8 mm, range = 49–61 mm). There are significant differences among SVLs for these populations (Kruskal–Wallis test = 30.5, 6 df, $P < 0.001$).

The body of each anole was opened by a longitudinal incision from vent to throat, and the digestive tract was removed by cutting across the anterior esophagus and rectum. The esophagus, stomach, and small and large intestines were slit longitudinally and examined under a dissecting microscope. The gallbladder, liver, and body cavity were also searched for helminths. Each helminth was initially placed in a drop of glycerol on a glass slide. Nematodes were identified from these temporary mounts. Trematodes, cestodes, and acanthocephalans were stained with hematoxylin and mounted in balsam for identification. Selected encysted nematode larvae and acanthocephalan cystacanths were embedded in paraffin, and histological sections were cut at 8 µm and stained with hematoxylin and eosin. Terminology follows that of Bush et al. (1997).

The helminth fauna of *A. cristatellus* from the British Virgin Islands consisted of 1 species of trematode, *Mesocoelium monas* (Rudolphi, 1819), 1 species of cestode, *Oochoristica maccoyi* Bursey and Goldberg, 1996, 6 species of nematodes, 4 of which were represented by mature individuals, *Parapharyngodon cubensis* (Baruš and Coy Otero, 1969), *Spauligodon anolis* (Chitwood, 1934), *Trichospirura teixeirai* (Baruš and Coy Otero, 1968), and *Rhabdias* sp., 2 of which were represented by larvae, *Physa-*

Table 1. Island of occurrence, number, prevalence, mean intensity, range, and mean abundance of helminths in 62 *Anolis cristatellus* from the British Virgin Islands.

Island Helminth	No. lizards	No. helminths	Prevalence (%)	Mean Intensity $\bar{x} \pm SD$	Mean Intensity Range	Mean Abundance ($\bar{x} \pm SD$)
Anegada	6					
Parapharyngodon cubensis		8	67	2.0 ± 1.4	1–4	1.3 ± 1.5
Porrocaecum sp. (larvae)		4	33	2.0 ± 1.4	1–3	0.7 ± 1.2
Centrorhynchus sp. (cystacanths)		20	17	20.0		3.3 ± 8.2
Beef	8					
Parapharyngodon cubensis		16	50	4.0 ± 2.2	2–7	2.0 ± 2.5
Spauligodon anolis		99	38	33.0 ± 32.1	12–70	12.4 ± 24.2
Trichospirura teixeirai		5	25	2.5 ± 2.1	1–4	0.6 ± 1.4
Porrocaecum sp. (larvae)		4	25	2.0		0.5 ± 0.9
Centrorhynchus sp. (cystacanths)		3	13	3.0		0.4 ± 1.1
Oligacanthorhynchidae (cystacanths)		8	38	2.7 ± 1.2	2–4	1.0 ± 1.5
Guana	3					
Parapharyngodon cubensis		8	67	4.0 ± 2.8	2–6	2.7 ± 3.1
Porrocaecum sp. (larvae)		8	67	4.0 ± 4.2	1–7	2.7 ± 3.8
Centrorhynchus sp. (cystacanths)		3	67	1.5 ± 0.7	1–2	1.0 ± 1.0
Necker	12					
Parapharyngodon cubensis		24	83	2.4 ± 2.2	1–8	2.0 ± 2.2
Trichospirura teixeirai		1	8	1.0		0.8 ± 0.3
Physaloptera sp. (larva)		1	8	1.0		0.8 ± 0.3
Porrocaecum sp. (larvae)		77	83	7.7 ± 8.0	2–28	6.4 ± 7.8
Centrorhynchus sp. (cystacanths)		8	25	2.7 ± 1.2	2–4	0.7 ± 1.3
Oligacanthorhynchidae (cystacanth)		1	8	1.0		0.1 ± 0.3
Norman	12					
Parapharyngodon cubensis		8	58	1.1 ± 0.4	1–2	0.7 ± 0.6
Porrocaecum sp. (larva)		1	8	1.0		0.1 ± 0.3
Centrorhynchus sp. (cystacanths)		60	75	6.6 ± 3.4	2–11	5.0 ± 4.2
Tortola	11					
Oochoristica maccoyi		1	9	1.0		0.1 ± 0.3
Parapharyngodon cubensis		20	55	3.3 ± 2.5	1–7	1.8 ± 2.5
Trichospirura teixeirai		8	27	2.7 ± 2.9	1–6	0.7 ± 1.8
Porrocaecum sp. (larvae)		13	27	4.3 ± 2.9	1–6	1.2 ± 2.4
Rhabdias sp.		2	18	1.0		0.2 ± 0.4
Centrorhynchus sp. (cystacanths)		27	36	6.8 ± 6.9	2–17	2.5 ± 5.1
Oligacanthorhynchidae (cystacanths)		2	18	1.0		0.2 ± 0.4
Virgin Gorda	10					
Mesocoelium monas		72	60	12.0 ± 6.3	5–23	7.2 ± 7.8
Parapharyngodon cubensis		18	80	2.3 ± 1.3	1–4	1.8 ± 1.5
Trichospirura teixeirai		4	10	4.0		0.4 ± 1.3
Porrocaecum sp. (larvae)		137	90	15.2 ± 25.0	1–77	13.7 ± 24.1
Centrorhynchus sp. (cystacanth)		1	10	1.0		0.1 ± 0.3
Oligacanthorhynchidae (cystacanths)		25	60	4.2 ± 5.1	1–14	2.5 ± 4.4

loptera sp. and *Porrocaecum* sp., and 2 species of acanthocephalans represented by cystacanths, *Centrorhynchus* sp. and an unidentified oligacanthorhynchid acanthocephalan. The specimens of *Rhabdias* sp. had damaged anterior regions and could not be identified to species. *Anolis cristatellus* represents a new host record for *O. maccoyi*, *T. teixeirai*, *Physaloptera* sp., *Porrocaecum* sp., and the oligacanthorhynchid cystacanths.

Representative helminths were placed in vials of alcohol and deposited in the U.S. National Parasite Collection (USNPC) Beltsville, Maryland: *Mesocoelium monas* 87534; *Parapharyngodon cubensis* 87535; *Spauligodon anolis* 87536; *Trichospirura teixeirai* 87537; *Physaloptera* sp.

87538; *Porrocaecum* sp. 87539; *Rhabdias* sp. 87540; *Centrorhynchus* sp. (cystacanths) 87541; oligacanthorhynchid cystacanths 87542.

Helminths were site specific. *Mesocoelium monas* and *O. maccoyi* were found in the small intestine. *Parapharyngodon cubensis* and *S. anolis* occurred in the large intestine. *Trichospirura teixeirai* was found in the gallbladder. *Rhabdias* sp. occurred in the lungs. The larva of *Physaloptera* sp. was found free in the stomach. Larvae of *Porrocaecum* sp., cystacanths of *Centrorhynchus* sp., and the unidentified oligacanthorhynchid acanthocephalan were encysted in the peritoneum of the coelom. The walls of these connective tissue cysts were constructed of several layers of fibrocytes and surrounding fibers.

Island of occurrence, number of lizards, number of helminths, prevalence, mean intensity, range, and mean abundance are presented in Table 1. Three helminth species were found on all islands, i.e., *Parapharyngodon cubensis*, *Porrocaecum* sp., and *Centrorhynchus* sp. There was no significant difference among prevalences by island for *Parapharyngodon cubensis* ($\chi^2 = 4.35$, 6 df, $P > 0.05$), but significant differences were found among prevalences by island for *Porrocaecum* sp. ($\chi^2 = 25.18$, 6 df, $P < 0.001$) and *Centrorhynchus* sp. ($\chi^2 = 15.92$, 6 df, $P < 0.05$). More anoles will need to be examined before the distribution differences for helminth species shown in Table 1 can be explained.

All helminths found in the present study are known from other anole hosts (Acholonu, 1976; Goldberg et al., 1997a, b; Torres Ortiz, 1980). These helminths fall into 2 groups: 1) species for which anoles are definitive hosts, i.e., *M. monas*, *O. maccoyi*, *Parapharyngodon cubensis*, *S. anolis*, *T. teixeirai*, and *Rhabdias* sp., and 2) species for which anoles are paratenic hosts, i.e., helminths occur only as immature stages and have no chance of completing their life cycles: *Porrocaecum* sp., *Centrorhynchus* sp., and oligacanthorhynchid cystacanths.

The only other populations of *A. cristatellus* examined for helminths are from Puerto Rico. Three species of trematodes, *Allopharynx puertoricensis*, *A. riopedrensis*, and *M. monas*; 4 species of nematodes, *Befilaria puertoricensis*, *S. anolis* (=*Pharyngodon anolis* sensu Acholonu, 1976), *Parapharyngodon cubensis* (=*Pharyngodon travassosi* sensu Acholonu, 1976), and *Rhabdias* sp.; and 2 species of acanthocephalans, *Centrorhynchus* sp. and *Lueheia inscripta*, have been reported from these populations (Chitwood, 1934; Cofresí-Sala, 1964; García-Díaz, 1966, Bain and Chaniotis, 1975; Acholonu, 1976; Torres Ortiz, 1980). Thus, British Virgin Island and Puerto Rican populations of *A. cristatellus* currently have 5 helminth species in common: *M. monas*, *S. anolis*, *Parapharyngodon cubensis*, *Rhabdias* sp., and *Centrorhynchus* sp. Because sample sizes for the populations of *A. cristatellus* examined to date have been small, more individuals will need to be examined before biogeographic patterns of the various helminth species can be evaluated.

We thank David Cannatella (Texas Memorial Museum, University of Texas–Austin) for permission to examine *Anolis cristatellus* for helminths and H. J. Holshuh (Veterinary Public Health, County of Los Angeles) for histopathological examination of encysted larvae.

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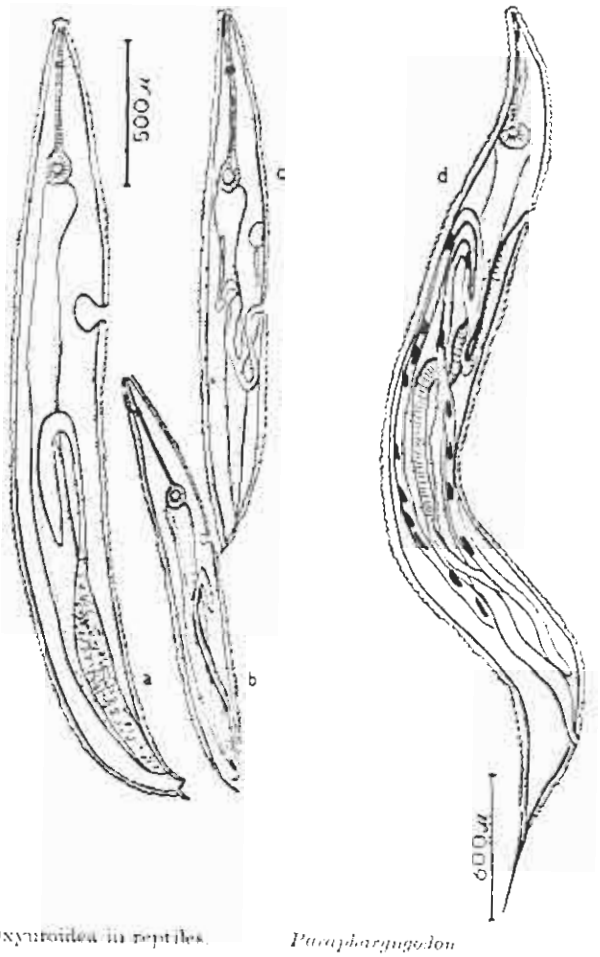


Oxyuroidea in reptiles *Parapharyngodon*

(Thought you might like to see what some actually look like.- ed.)

The Methiini of the West Indies (Coleoptera: Cerambycidae) with notes on the circum-Caribbean species

T. KEITH PHILIPS and MICHAEL A. IVIE

Ent. scand.

Philips, T. K. & Ivie, M. A.: The Methiini of the West Indies (Coleoptera: Cerambycidae) with notes on the circum-Caribbean species. *Ent. scand.* 29: 57-87. Copenhagen, Denmark. May 1998. ISSN 0013-8711.

The Methiini of the West Indies are revised. *Cyanomethia pseudothonalmus*, new genus, new species and *Methia jamaicensis* new species are described. *Methia pusilla*, *M. constricticollis*, *M. impressicollis*, *M. insularum*, *M. pallida*, *M. pulchra*, *M. punctata*, and *M. rhizophorae* are new synonyms of *M. necydalea*. Keys to genera of Methiini and species of *Methia* in the West Indies are given and the biology and morphological variation of the genus *Methia* discussed. A phylogenetic analysis of the Methiini is conducted to determine relationships among the genera, and the zoogeographic patterns of species found in the West Indies is included.

T. K. Philips* & M. A. Ivie, Department of Entomology, Montana State University, Bozeman, MT 59717, U.S.A. **Current address:* Museum of Biological Diversity, Department of Entomology, The Ohio State University, 1315 Kinnear Road, Columbus, OH 43212, U.S.A. (philips.3@osu.edu)

Introduction

The tribe Methiini within the subfamily Cerambycinae has been subject to a great deal of taxonomic confusion since Fabricius (1798) described the first species in what is now the Lamiinae (Monné 1993 and citations within). The subfamilial placement and tribal limits of the Methiini have stabilized following a variety of views (Cazier & Lacey 1952, Linsley 1962, Martins et al. 1966, Chemsak & Linsley 1967). Most recently, Martins & Carvalho (1984) reduced the number of methiine genera to five, by resurrecting the Xystrocerini and the Oemini. Species of methiines have been revised for America north of Mexico (Linsley 1962), southern North America (Hovore 1987), Mexico and Central America (Chemsak & Linsley 1964b), South America (Martins 1981), Curaçao, Bonaire, and Aruba (Gilmour 1968) and various parts of the West Indies (Cazier & Lacey 1952, Zayas 1975, Villiers 1980a). These treatments varied in their depth and in the species concept used. In this study, we revise the Methiini of the West Indies and the related species of *Methia* occupying lowlands around the Caribbean Sea and Gulf of Mexico. Further, we provide a hypothesized phylogeny for the genera of Methiini.

Eleven species of *Methia* Newman and one species of *Tessaropa* Haldeman have been described from the West Indies and circum-Caribbean region. The problems described below regarding the species-level classification of *Methia* have resulted from species which are extremely variable, both intraspecifically and intersexually, in characters such as color, degree of dorsal and ventral eye separation, and elytral shape and sculpture. Species delimitations based on these highly variable characters, compounded by problems associated with small type series and possible assumptions of endemism, have contributed to the current state of taxonomic confusion. These problems are probably not limited to *Methia*, but are relevant to many different groups of organisms in the West Indies.

Materials and methods

This study is based upon an examination of over 1,500 adult specimens of *Methia* and about 60 specimens of other closely related genera. Of these, 540 are from the West Indies, sensu stricto. It should be noted that although this project has brought together nearly all available specimens from the West Indies, there is a very strong geographic collecting bias. Over 1/3 of the specimens examined are from the Virgin Islands. There were

less than 15 specimens each from the Cayman Islands and the individual islands of the Lesser Antilles. However, because the variability exhibited in the larger series overlapped that of the small series, the material was sufficient to make a good estimate of species limits based on consistent morphological characters.

The following institutions and individuals loaned or made available material for this study, identified in the text with the accompanying codens:

BPBM – Bishop Museum, Honolulu, HI (S. Miller); BMNH – The Natural History Museum, London (R. Pope & J. Marshall); CASC – California Academy of Sciences, San Francisco, CA (D. H. Kavanaugh); CJSC – J. Cope, private collection, San José, CA; CNCI – Canadian National Insect Collection, Ottawa, ON (J. McNamara); DHCT – D. Heffern, private collection, Houston, TX; DMAG – Museum and Art Gallery, Doncaster (P. Skidmore); EJGC – E. J. Gerberg, private collection, Gainesville, FL; FZCC – Fernando de Zayas Collection, Havana, Cuba; FSCA – Florida State Collection of Arthropods, Gainesville, FL (M. Thomas & B. Beck); FTHC – F. T. Hovore, private collection, Santa Clarita, CA; IESC – Instituto de Ecologia y Systematica, Academia de Ciencias, Habana, Cuba (Luis F. de Armas); IJSM – Natural History Museum, Institute of Jamaica, Kingston, Jamaica (T. H. Farr); IREC – Institut de Recherches Entomologique de la Caraibe, Guadeloupe (F. Chalumeau); IZAV – Universidad Central de Venezuela, Maracay, Venezuela; (L. Joly); JMIC – J. Micheli, private collection, Ponce, Puerto Rico; MHND – Museo National de Historia Natural, Santo Domingo, Dominican Republic (L. Dominguez & R. Rimoli); CMNC – Canada Museum of Nature, Ottawa, ON (B. Gill); NMNH – National Museum of Natural History, Washington (T. J. Spilman); OSUC – The Ohio State University Collection of Insects and Spiders, Columbus, OH (C. A. Triplehorn); RHTC – R. H. Turnbow, private collection, Fort Rucker, AL; RSMC – R. S. Miller, private collection, Belgrade, MT; TAMU – Texas A&M University, College Station, TX (E. G. Riley); TMPC – T. McCabe, private collection, Albany, NY; UCBC – California Insect Survey, University of California, Berkeley, CA (J. A. Chemsak); UCDC – Bohart Museum, University of California, Davis, CA (R. O. Schuster); UPRR – University of Puerto Rico Agricultural Experiment Station, Rio Piedras, Puerto Rico (R. Inglés); UVCC – University of Vermont Collection, Burlington, VT (R. Bell); VIER – Virgin Islands Ecological Research Station, Virgin Islands National Park, St. John, Virgin Islands (J. Miller); WHTC – W. H. Tyson, private collection, Fresno, CA; ZMUC – Zoological Museum, University of Copenhagen, Copenhagen, Denmark (O. Lomholdt & O. Martin). Material deposited in our private collections is indicated TKPC and MAIC.

Species limits were determined by morphological analysis using the criteria of Whitehead (1972), a practical species definition based on available data from adult morphology and distribution. Initially, all available specimens from each Caribbean island were examined and sorted into groups based on their external similarity. Internal characters were then examined for consistency within and between these groups. Populations from different islands were then compared, and lastly, comparisons were made with species and specimens present on adjacent areas of North and South America. Due to the large amount of sexual dimorphism, males were first critically examined and the resulting hypotheses about species limits tested with females. Types of all species were examined except for *Methia trium* Gilmour.

Dissections were made by soaking specimens in hot distilled water (90-99°C) to soften tissues. Gross structures were then carefully removed using minuten pins. Cuticular structures were cleared in lactic acid or a weak solution of sodium hydroxide. Parts were then neutralized, rinsed with distilled water, and stored in glycerin. Structures were studied on temporary slide mounts in glycerine and illustrations were made using drawing tubes on Wild M20 compound and Wild M5 dissecting microscopes. Measurements were made at 50x, using a micrometer eyepiece with a scale interval of 0.1 mm. Dissected structures were placed in genitalia vials or glued to a card, and placed on the specimen pin after examination. Wing venation was homologized with Ponomarenko (1973) and Doyen (1966). Genitalic structures were homologized with Sharp & Muir (1912) for males and Tanner (1925) for females. Label data was recorded using the conventions of Hayek (1973).

A cladistic analysis of adults was conducted to hypothesize relationships among the methiine genera. Five of six methiine genera were studied as *Paratessaropa* Zajciw was unavailable. Representatives of two or three species of each ingroup genus were included, except in *Tessaropa* and the monotypic *Cyanomethia* gen. n. *Oeme rigida* (Say), a member of the Oemini, was used as the outgroup. Twenty-five bipolar characters were analyzed unweighted with Hennig86, version 1.5 (Farris 1988), using the implicit enumeration (ie*) option. Character state distributions were examined with Clados, version 1.2 (Nixon 1992).

Tribe METHIINI Thompson

Methiinae Thompson, 1860: 127, 364.
Methiitae; Thomson 1864: 92, 387.
Methiides; Lacordaire 1872: 216.
Methiini; LeConte 1873: 347; LeConte & Horn 1883:

333; Hamilton 1896: 13; Lameere 1901: 315; Gahan *in* Distant 1904: 108; Gahan 1908: 143; Aurivillius 1912: 38 (cat.); Craighead 1923: 38; Bradley 1930: 228, 131; Linsley 1932: 120; 1940: 29; 1962: 13; Arnett 1962: 859, 879; Chemsak & Linsley, 1964b: 40; Martins et al. 1966: 197; Chemsak & Linsley 1967: 28; Gilmour 1968: 88; Hatch 1971: 99; Fragoso 1978: 25; Villiers 1980a: 266; Martins & Carvalho 1984: 214; Browne et al. 1993: 41; Monné 1993: 23.
Oemini; Linsley 1961b: 629 (in part).

Diagnosis. – The Methiini can be separated from the Xystrocerini by having mesocoxae without tubercles or ridges, the abdomen of males with only five distinctly visible ventrites, the scape apex usually without a cicatrix, the prosternal process apex free (not in close contact with the mesosternum and often directed perpendicularly to the longitudinal axis of the body ventrally (absent in *Styloxus*)), and the sides of the head straight (instead of slightly rounded) behind the eyes. Methiini are separated from the Oemini (and the Xystrocerini), by the subacuminate ultimate palpomeres, the usually reduced elytra, the medially confluent procoxae contacting each other medially, and the radular form of the female terminalia. Additionally, the Methiini are restricted to the New World.

Description. – Form elongate, slender to short and robust, sometimes slightly flattened; head and sometimes pronotum and elytra distinctly punctate. Head short; front vertical, clypeus very short, palpi unequal and sometimes very short, maxillary palpi slender, sometimes reduced in length, distal palpomere tapered, subacuminate, acute to somewhat truncate at apex; ligula feebly emarginate; vertex moderately to deeply impressed between antennal bases; antennae slender throughout, usually longer than body in both sexes, but ranging from about as long as body in female to over twice as long as body in the male; antennomeres not spinose at their apices, scape relatively robust, sometimes with an apical cicatrix; second antennomere very short, sometimes wider than long; third antennomere longer than scape, subequal to or slightly shorter than fourth antennomere; eyes small to large, finely to moderately granulate, deeply emarginate, or occasionally completely divided into separate upper and lower lobes, lower lobe distinctly larger than upper lobe; eyes usually distinctly separated above and below, ventral eye separation wider than dorsal separation, occasionally in contact dorsally. Pronotum subcylindrical or rounded, although sometimes irregularly so with a slight obtuse projection laterally; length to width subequal but sometimes distinctly longer than wide or slightly wider than long, sides usually slightly rounded; scutellum about as long as broad, broadly to narrowly rounded at apex, often with a slight groove or more broadly shaped, longitudinally oriented depression. Elytra usually abbreviated to various degrees, narrowing apically and usually separated along suture for most of their lengths, rarely strongly dehiscent; apices rounded although more broadly so laterally; wings with cubital vein forked (CuA and AA + CuA present). Anterior coxae ventrally prominent, subconical, strongly angulate externally, open posteriorly, confluent or separated by a narrow, often laminiform prosternal process, trocantin large, conspicuous; intermediate coxal cavities open to epimera; metepisterna broad in front, narrowing posteriorly. Abdomen usually elongate, rarely strongly abbreviated; female abdomen usually modified with fifth ventrite deeply, angularly notched ventrally; male sixth ventrite exposed. Legs slender, moderate to elongate in length, femora slightly to strongly clavate although hind femora sometimes very narrow and subparallel; tibia longer than femora; tarsi slender, subcylindrical to broad and slightly flattened, usually very short, metatarsi ranging from about 1/6 to 2/3 the length of the metatibia.

Discussion. – Species placed in the Methiini were described in what is now the Lamiinae by Fabricius (1798). This view was followed by Thomson (1860), when he erected the Methiini, and appeared as late as 1952 (Cazier & Lacy 1952). Gahan (1904) was the first to place the Methiini in the Cerambycinae and his view has been confirmed by various workers (for e.g. Linsley 1962, Martins & Carvalho 1984). The placement of the Oemini has varied over the years, being considered independent until a relationship was suggested by various workers (Gahan 1904 and 1908, Aurivillius 1912, Craighead 1923) and the two were formally synonymized by Linsley (1962). After the Western Hemisphere Methiini in this broad sense were revised by Martins et al. (1966) and Chemsak & Linsley (1967), Martins & Carvalho (1984) removed the Oemini and Xystrocerini, leaving the Methiini composed of five genera to which we add a sixth.

Two genera of methiines are here recognized from the West Indies, *Methia* Newman and *Cyanomethia* gen. n. Species possibly belonging to either

Tessaropa Haldeman and/or *Coleomethia* Linsley may occur in Cuba (see 'Species *incertae sedis*' below). *Methia* is a relatively large genus with 44 currently recognized species, reduced by eight (to 36), in this study. All are small, delicate beetles, with most species ranging from 4 to 9 mm in length, but some, such as *M. mormona* Linell, may reach a length of 15 mm. Found only in the New World, the genus is distributed from Argentina north through Central America to southern Idaho and Virginia. In addition to the 12 previously recognized species recorded from the West Indies and circum-Caribbean region, four were described from South America, with the remainder from the southern USA and Mexico. *Cyanomethia* is presently known only from St. John, U.S. Virgin Islands.

Key to the genera of West Indian METHIINI (sensu Monné 1993)

1. Eye facets small (~0.02 mm diameter); second antennomere transverse (length 2.5-3.5x width); first metatarsomere short (length < 2x width) 2
– Eye facets large (~0.04 mm diameter); second antennomere elongate (length 2.0x or less width); first metatarsomere long (length > 2x width), head as in Figs 1-6 ..... *Methia*
2. Elytra strongly rugose and costate; wings with four anal veins; head as in Figs 7-8..... ..... *Cyanomethia*
– Elytra weakly or not costate; wings with three anal veins..... 3
3. Male abdomen variably abbreviated; females with distal antennal segments (8 to 11) thickened; posterior femora of both sexes elongate (nearly parallel sided) and not clavate *Coleomethia**
– Male abdomen elongate; females with distal antennal segments narrowed, posterior femora relatively stout and feebly clavate..... *Tessaropa***

* not recorded from the West Indies, but possible; see below under '*Species incertae sedis*'.
** recorded but not confirmed from the West Indies; see below under '*Species incertae sedis*'.

Methia necydalea (Fabricius)

[Figs 1-6, 15-22, 25-30, 33-36, 39-55, 58-71, 92, 97)

Saperda necydalea Fabricius, 1798: 148. Holotype examined (ZMUC).

Saperda necydalina Fabricius, 1801: 332 [unjustified emendation]. Schoenherr 1817: 439.

Methia necydalea: Galian 1895: 122; Aurivillius 1912: 39; Leng & Mutchler 1914: 444 (in part, distr.); Fisher 1932: 7; Wolcott 1936: 259 (hosts); 1941: 98; 1948: 334; 1950: 334; Beatty 1944: 141 (distr.); Blackwelder 1946: 559 (in part); Ramos 1946: 41; Fattig 1947: 7; Cazier & Lacy 1952: 46, fig. 13; Linsley 1962: 37; Gilmour 1963: 96; 1968: 97; Chemsak & Linsley 1964a: 159; 1982: 12; Chemsak 1966: 211; 1967: 182 (distr.); 1969: 186 (distr.); Miskimen & Bond 1970: 94; Zayas 1975: 52; Villiers 1980a: 269; 1980b: 130; Monné 1993:27.

Methia necyaalea: Wolcott 1923: 109 [misspelling].

Thia pusilla Newman, 1840: 18. Lectotype (BMNH) here designated, labeled: Lectotype *Methia pusilla* desig. Philips & Ivie 1997. LeConte 1878: 470 (distr.). **Syn. n.**

Methia pusilla: Newman 1842: 418; LeConte 1852: 144; White 1855: 243; Chevrolat 1862: 256; Thomson 1864: 92; Lacordaire 1872: 467; LeConte 1873: 348; Horn 1885: 6; Schwarz 1888: 93 (hosts); Fleutiaux & Sallé 1889: 468; Gundlach 1891: 218; Leng & Hamilton 1896: 162; Castle & Laurent 1896: 304 (distr.); Craighead 1923: 41 (larva); Linsley 1940: 37; 1962: 36 (fig. 15); Cazier & Lacy 1952: 46; Gilmour 1968: 94; Turnbow & Hovore 1979: 220; Turnbow & Franklin 1980: 341; Turnbow & Wappes 1981: 75 (distr.); Chemsak & Linsley 1982: 12; Monné 1993: 28; Yanega 1996: 45.

Methia constricticollis Schaeffer, 1908: 351. Holotype USNM. Aurivillius 1912: 39; Linsley 1962: 31; Chemsak & Linsley 1964a: 159 (distr.); 1964b: 57; 1982: 12; Gilmour 1968: 96; Turnbow & Wappes 1978: 367 (hosts); 1981: 75; Hovore et al. 1987: 295; Chemsak & Feller 1988: 181; Monné 1993: 24. **Syn. n.**

Methia impressicollis Chemsak, 1966: 211. Holotype USNM. Gilmour 1968: 96; Chemsak & Linsley 1982: 12; Monné 1993: 26. **Syn. n.**

Methia insularum Chemsak, 1966: 210. Holotype USMN. Gilmour 1968: 97; Monné 1993. 26. **Syn. n.**

Methia pallida Fisher, 1932: 6. Holotype USNM. Blackwelder 1946: 559; Chemsak 1966: 211; Gilmour 1968: 94; Chemsak & Linsley 1982: 12; Monné 1993: 27. **Syn. n.**

Methia pulchra Chemsak & Linsley, 1964a: 159. Holotype USMN. Gilmour 1968: 96; Chemsak & Linsley 1982: 12; Monné 1993: 27. **Syn. n.**

Methia punctata LeConte, 1873: 240. Lectotype (IESC) here designated, labeled: 52 Methia pusilla / Lectotype Methia punctata desig. M. A. Ivie 1990 / = Methia necydalea Fabricius det M. A. Ivie. Paralectotype in IESC. Lameere 1883: 57 (cat.); Gundlach 1894: 327; Leng & Hamilton 1896: 163; Aurivillius 1912: 39; Leng & Mutchler 1914: 444 (distr.); 1917: 209; Wolcott 1923: 109; 1950: 334; Blackwelder 1946: 559; Gilmour 1968: 99; Zayas 1975: 53; Chemsak & Linsley, 1982: 12; Monné 1993: 27. **Syn. n.**

Methia rhizophorae Chemsak & Feller, 1988: 181. Holotype USNM. Monné 1993: 28. **Syn. n.**

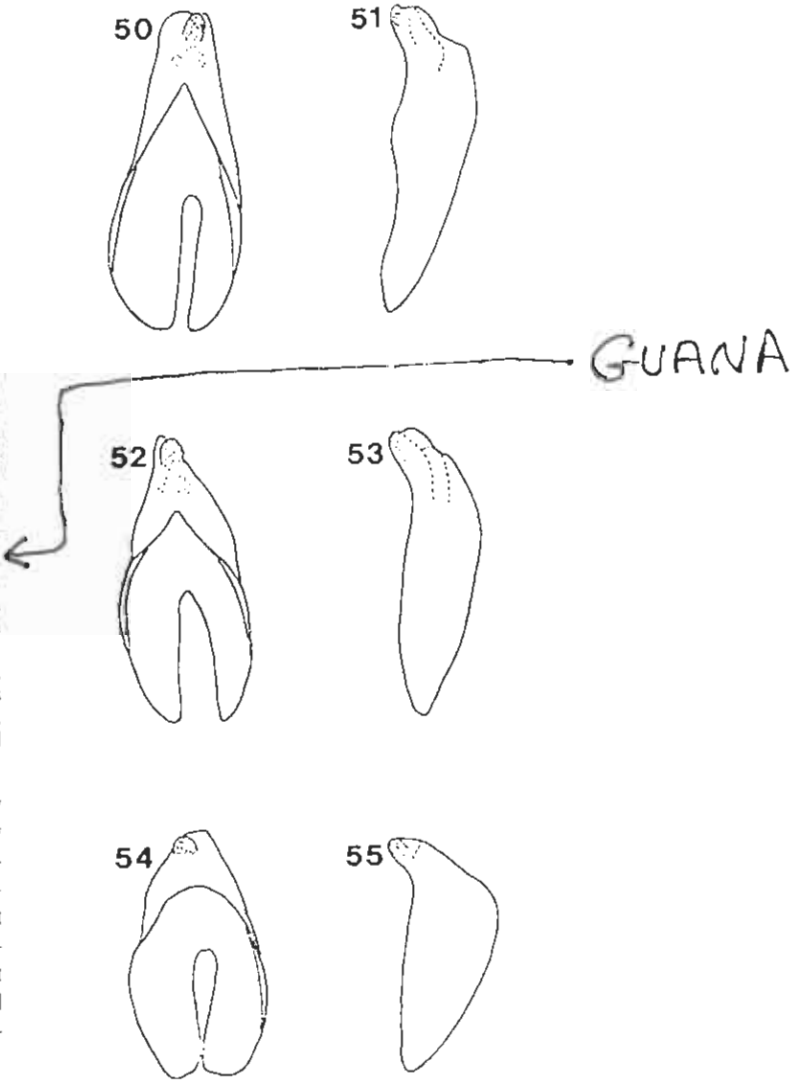
Material studied. – Holotypes/lectotypes examined: *Methia constricticollis* (female, USNM); *Methia impressicollis* (female, NMNH) ; *Methia necydalea* (sex?, ZMUC); *Methia punctata* (male, IESC); *Methia pusilla* (male, BMNH). Paratypes/paralectotypes examined: *Methia rhizophorae* (1 male & 1 female, UCBC); *Meth-*

ia pulchra (1 male, UCBC); *Methia punctata* (1 female, IESC); *Methia insularum* (2 males & 6 females, UCBC); *Methia pallida* (2 females, NMNH).

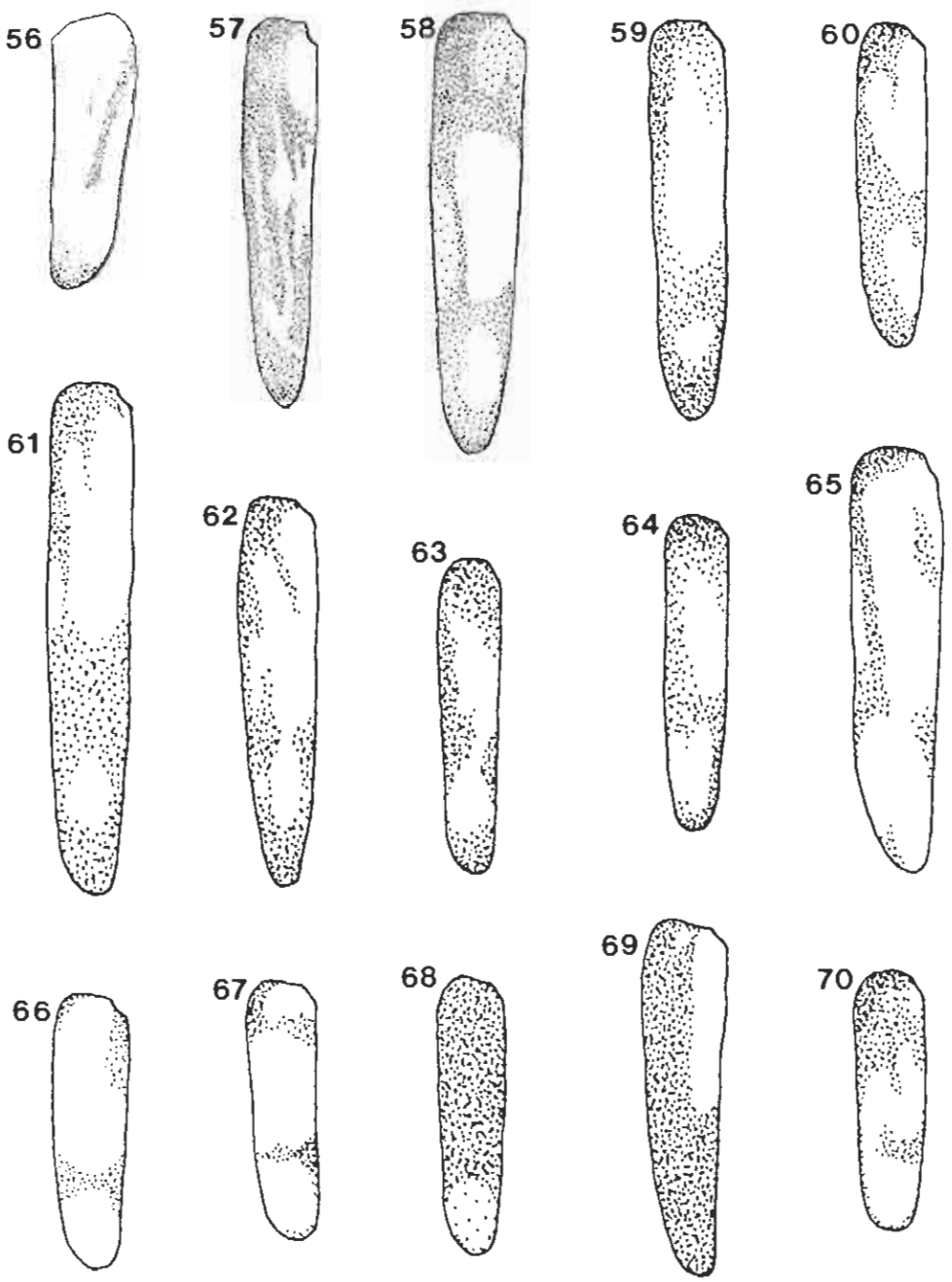
Additional material examined: UNITED STATES: 2, Alabama (RHTC); 43, Florida (UCBC, CNCI, CMNC, DHCT, RHTC, MAIC, FTHC); 12, Georgia (RHTC, CMNC, UCBC); 1, Louisiana (DHCT); 1, Mississippi (MAIC); 1, South Carolina (TKPC); 2, North Carolina (CMNC); 105, Texas (RHTC, DHCT, CMNC, UCBC, TAMU, FTHC); 2, Virginia (NMNH). MEXICO: 4, Chiapas (UCBC); 3, Oaxaca (UCBC); 2, Campache (UCBC); 2, San Luis Potosi (UCBC, MAIC); 1, Tamaulipas (UCBC); 21, Nuevo León (MAIC, CMNC, UCBC). BAHAMAS: 13, Great Exuma (TMPC); 2, Fortune Is. (MAIC); 6, Andros Is. (UCBC, MAIC); 29, South Bimini Is. (CASC, DMAG, NMNH, UCBC); 1, Mayaguana Is. (UCBC). CUBA: 26 (BMNH, CASC, FZCC, IESC, JMIC). CAYMAN ISLANDS: 10, Grand Cayman (BMNH, CNCI, UCDC, EJGC); 3, Cayman Brac (BMNH); 1, Little Cayman (BMNH). HAITI: 8 (MAIC, NMNH). DOMINICAN REPUBLIC: 43 (NMNH, UCDC, UCBC, BMNH, MHND, TKPC, MAIC); 4, Mona Is. (UPRR, NMNH). PUERTO RICO: 90 (CJSC, IREC, JMIC, NMNH, RHTC, UCBC). VIRGIN ISLANDS: 41, Guana Is. (BPBM, MAIC); 38, St. Thomas (RSMC, NMNH, MAIC); 68, St. John (NMNH, UCBC, VIER, MAIC); 28, St. Croix (UCBC, WHTC, NMNH, MAIC). LESSER ANTILLES: 1, Grenada (BMNH); 3, St. Barthelemy (IREC); 3, St. Martin (IREC); 1, Antigua (IREC); 3, St. Lucia (IREC, FSCA); 3, St. Vincent (IREC); 1, Dominica (BMNH); 1, Nevis (RSMC); 1, Les Saintes (MAIC); 5, Guadeloupe (IREC, JMIC); 6, Marie Galante (IREC). For a more detailed listing see Philips (1990).

Diagnosis. – *Methia necydalea* has a relatively long postmentum (Figs 30, 33-36) and a relatively smoothly rounded male paramere cleft (Figs 39-49). A few specimens of *M. necydalea* (Figs 44-46) approach the cleft depth of *M. jamaicensis*, but never with quite the same degree of apical angulation. This species also has a great range in cleft depth, ranging from no cleft to a cleft 3/4 the total length of the main paramere body. The elytral pattern is extremely variable (Figs 58-70).

Description. – Male. Length 3.9-8.3 mm. Form elongate slender to slender. Integument dark brown to pale testaceous. Elytra color and pattern extremely variable but usually brown at humeral angle, transversely or nearly so at about apical 1/3, and at apex (Figs 58-70). Head at eyes wider than pronotum, sometimes inflated on vertex behind eyes, front areolate-rugose, less so on vertex, usually densely, irregularly punctate at posterior margin; upper and lower eye lobes separate or joined by one or two rows of facets (Figs 11-12); antennae extending beyond abdominal apex by about four segments; apex of scape sometimes with a slight tooth; postmentum of the labium width to length ratio about 2.5:1, prementum lobes triangular shaped to parallel sided, sometimes relatively blunt with rounded apices (Figs 30, 33-36). Pronotum slightly broader than long, sides broadly, sometimes irregularly rounded, parallel or subparallel at apex and base; base occasionally very strongly constricted (Figs 15-22), narrower than at apex; disc usnally fine to coarsely, densely rugose-



Figs 50-55. Variability in shape of median lobe of *Methia necydalea*, ventral (left) and lateral (right) views: (50-51) Puerto Rico; (52-53) Puerto Rico; (54-55) Marie Galante.



Figs 56-70. Elytral patterns in *Methia* spp., left elytron except where indicated: (56) *M. trium* right elytron, Curaçoa; (57) *M. jamaicensis*, Jamaica; (58-70) *M. necydalea*: (58) Cayman Islands;(59) Bahamas; (60) St. Thomas, U.S. Virgin Islands; (61) Guadeloupe; (62) Puerto Rico; (63) Puerto Rico; (64) Puerto Rico; (65) St Croix, U.S. Virgin Islands; (66) Texas; (67) Florida; (68) Florida; (69) Belize; (70) Belize.

punctate, slightly to moderately impressed transversely near anterior and posterior margins; often two very slight, irregularly shaped callosities at anterior 1/4 on each side of midline, sometimes extended longitudinally towards base, usually a relatively smooth, longitudinal maculation medially around basal 1/3 or 1/4, rarely slightly raised; callosities and maculation, even if not present, usually relatively paler than surrounding areas; sometimes also relatively pale in longitudinal band from and including callosities to just before basal transverse impression, band expanded transversely laterally near middle; sometimes relatively paler at apical and basal margin. Stridulatory plate of mesonotum smooth, without a median line; prosternum very finely rugose-punctate with sparse long erect setae; mesosternum more densely, finely rugose-punctate with moderately dense suberect setae; metasternum finely, regularly punctate, with moderately dense suberect setae. Elytra extending past second abdominal segment, rounded at apex; each elytron sometimes distinctly tricostate, costae becoming finer towards apex; pubescence pale, suberect, occasionally some erect setae; each elytron sometimes almost completely either pale testaceous or dark brown, with humeral or apical margin contrasting light or dark; more usually a pattern consisting of a relatively dark humeral angle, an irregular, transverse dark band at apical 2/5, and a dark apex; transverse band sometimes split at middle, with outer part sometimes extending longitudinally to humeral angle and inner part (located near or including suture), sometimes extending longitudinally to apex; pattern sometimes consisting of relatively pale longitudinal areas on disc at basal 1/3 to middle and at apical 1/5, with other areas darker. Abdomen moderately, finely, evenly punctate with moderately dense setae, fifth ventrite broadly emarginate. Femora finely, transversely plicate. Male paramere as in Figs 39-49. Male median lobe as in Figs 50-55. Maxilla and labium as in Figs 25-30, 33-36. Wing as in Fig. 97. Dorsal habitus Fig. 71.

Female. Length 4.7-9.6 mm. Usually larger, often with more elongate elytra. Antennae extending past the abdomen by 4-5 segments. Apex of last abdominal ventrite deeply emarginate. Female genitalia as in Fig. 92.

Distribution. – This taxon is a very wide ranging circum-Caribbean species. It has been recorded as far north as Virginia south along the east coast to Florida, around the Gulf of Mexico and Caribbean coast to Belize. In addition to the States mentioned in the 'Material studied', Linsley (1962) records it from Arkansas. It also occurs throughout the West Indies except Jamaica and Barbados (Bennett & Alam 1985) (see 'Material studied' for more detail).

Host range. – *Methia necydalea* has a very broad host range. In Puerto Rico, it has been collected on dead Guamá (*Inga fagifolia* (L.) Willd.), a member of the Mimosaceae. In Twin Keys, Belize, it is associated with red mangrove (*Rhizophora mangle* L.), black mangrove [*Avicennia germinans* (L.) Stearn], white mangrove [*Laguncularia racemosa* (L.) Gaertn. f.], and buttonwood [*Conocarpus erectus* (L.)] (Chemsak & Feller 1988). Other hosts include *Celtis* Tourn. ex L. (Turnbow & Wappes 1978), *Zanthoxylum* L. (Turnbow & Wappes 1981), and probably also *Eugenia* Mich. ex L. and *Amyris* P. (Wolcott 1950). Larvae have been described and were collected with adults in small branches of *Taxodium* Richard in Georgia (Craighead 1923). Turnbow & Hovore (1979) report rearing specimens from dead branches and twigs of an oak (*Quercus virginiana* Miller). These verified hosts of *M. necydalea*, belonging to both gymnosperms and angiosperms, illustrate a very broad host range.

Discussion. – Several names have been proposed for specimens referable to *M. necydalea*. The earliest described species of *Methia* was *Saperda necydalea* Fabricius (1798) from St. Thomas in what is now the U.S. Virgin Islands. In 1840, Newman described *Thia pusilla* from two specimens collected in East Florida and later (1842) proposed *Methia* for the preoccupied *Thia*. *Methia punctata* was based on two specimens from Cuba and the Dominican Republic (LeConte 1873). The type locality of *Methia constricticollis* Schaeffer, based on a single specimen, is Brownsville, Texas (Schaeffer 1908) and three specimens from Haiti were named *M. pallida* by Fisher (1932). Chemsak & Linsley (1964a) described *M. pulchra* based on three individuals from Cozumel and Isla Mujeres, Quintana Roo, Mexico. Chemsak (1966) continued Carihhean work by describing *Methia insularum* and *M. impressicollis* from Virgin Gorda and Jost van Dyke in the British Virgin Islands (based on 12 and one specimens respectively). *Methia rhizophorae* Chemsak & Feller (1988) from Belize, was the latest name proposed for five specimens.

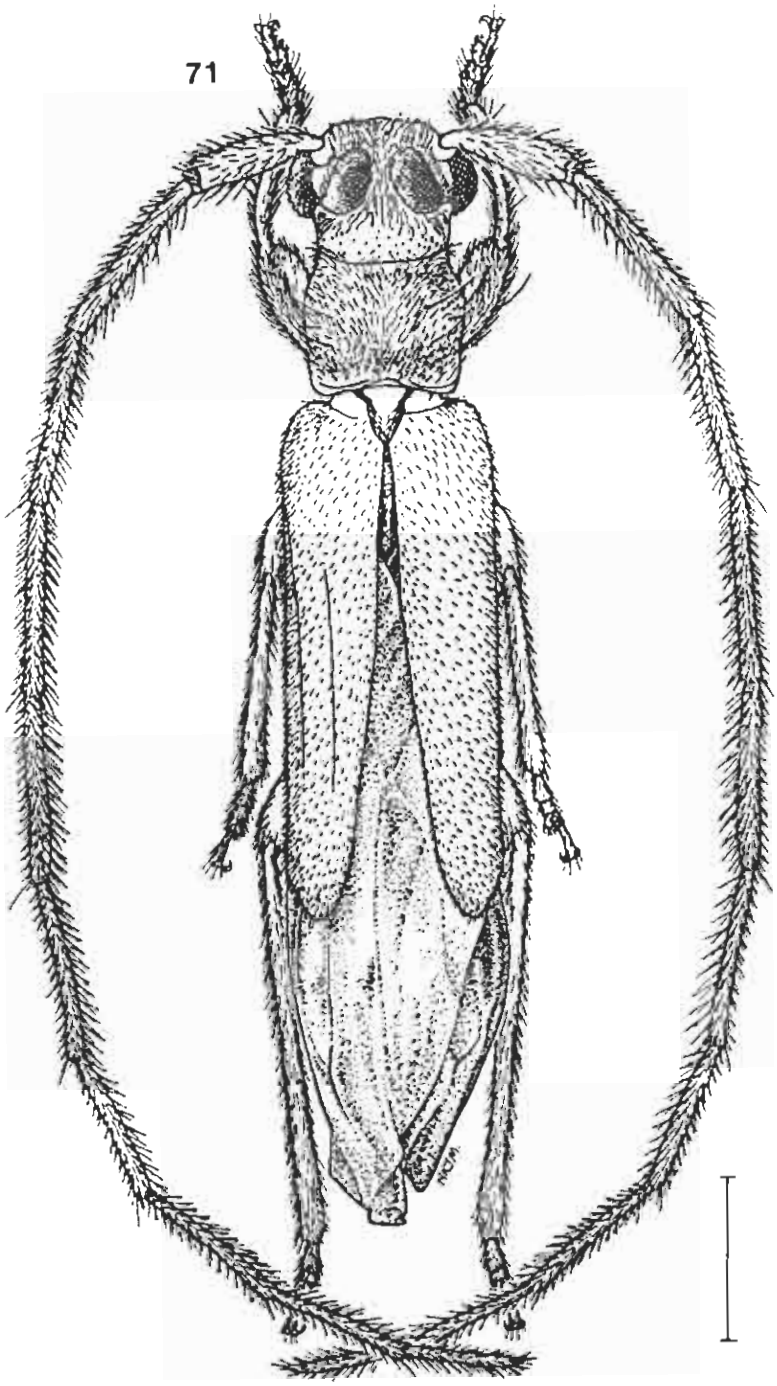
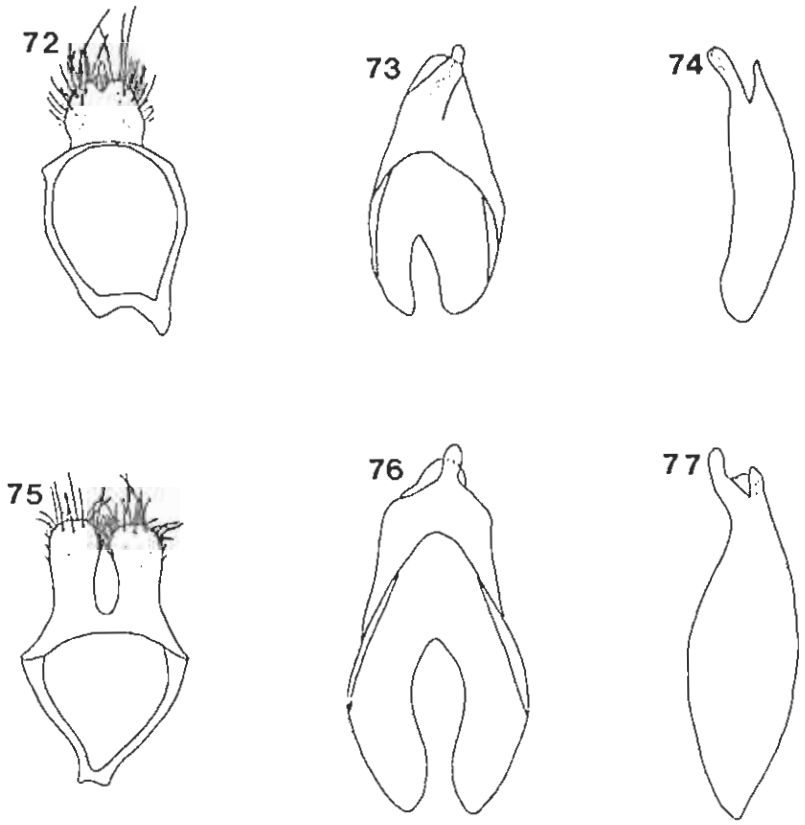


Fig. 71. Dorsal habitus of *Methia necydalea*. ♀. Scale bar = 1.0 mm.

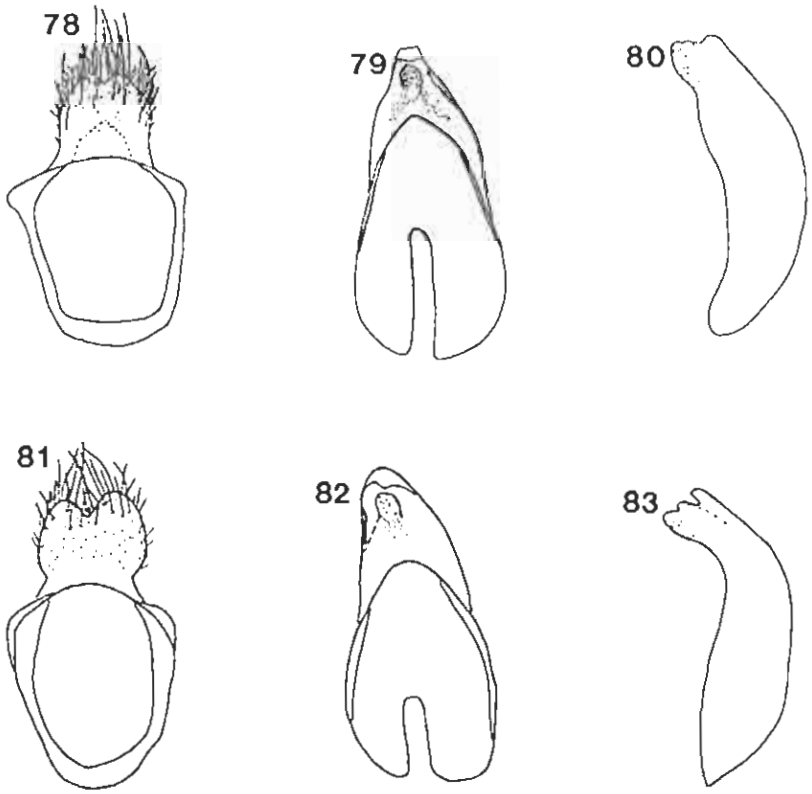


Figs 72-77. Male genitalia: paramere (left), aedeagus ventral (middle), aedeagus, lateral (right): (72-74) *Tessaropa tenuipes*; (75-77) *Styloxus bicolor*.

This project was precipitated by the fact that three species were described from the Northern Virgin Islands, and as more and more V.I. material became available, the extent of continuous variation grew. As the existence of synonymies became increasingly clear, the limits of described species were called into question from an ever widening area.

The species synonymized here were differentiated with variable characters, such as color, elytral shape, eye facet connection, and degree of basal pronotal constriction. Another major factor contributing to the number of synonymies of *M. necydalea* is the small series sizes used to describe new species, and additionally, these series often being collected from a single locality. Specimens within a series with the same label data are sometimes very similar in shape and color. Although many authors did not examine types, this action may not have affected the number of descriptions. Indeed, the number of species described does not seem unusual, in light of the extremely variable nature of this species. This variability is illustrated by long series, which are often extremely diverse. For example, Cazier & Lacy (1952) collected 255 specimens from Bimini, Bahamas and noted the wide range of size and elytral color pattern within this series.

Many morphological forms of *M. necydalea* are present in the West Indies. Both *M. pallida* and *M. insularum* are based upon pale individuals. The holotype of *M. impressicollis* is a teneral, poorly preserved and distorted female. Other species are based on different phenotypes and characterized by highly variable characters as discussed previously. Due to a lack of geographic trends in these



Figs 78-83. Male genitalia; paramere (left), aedeagus ventral (middle), aedeagus, lateral (right): (78-80) *Cyanomethia pseudothonalmus*; (81-83) *Colcomethia xanthocollis*.

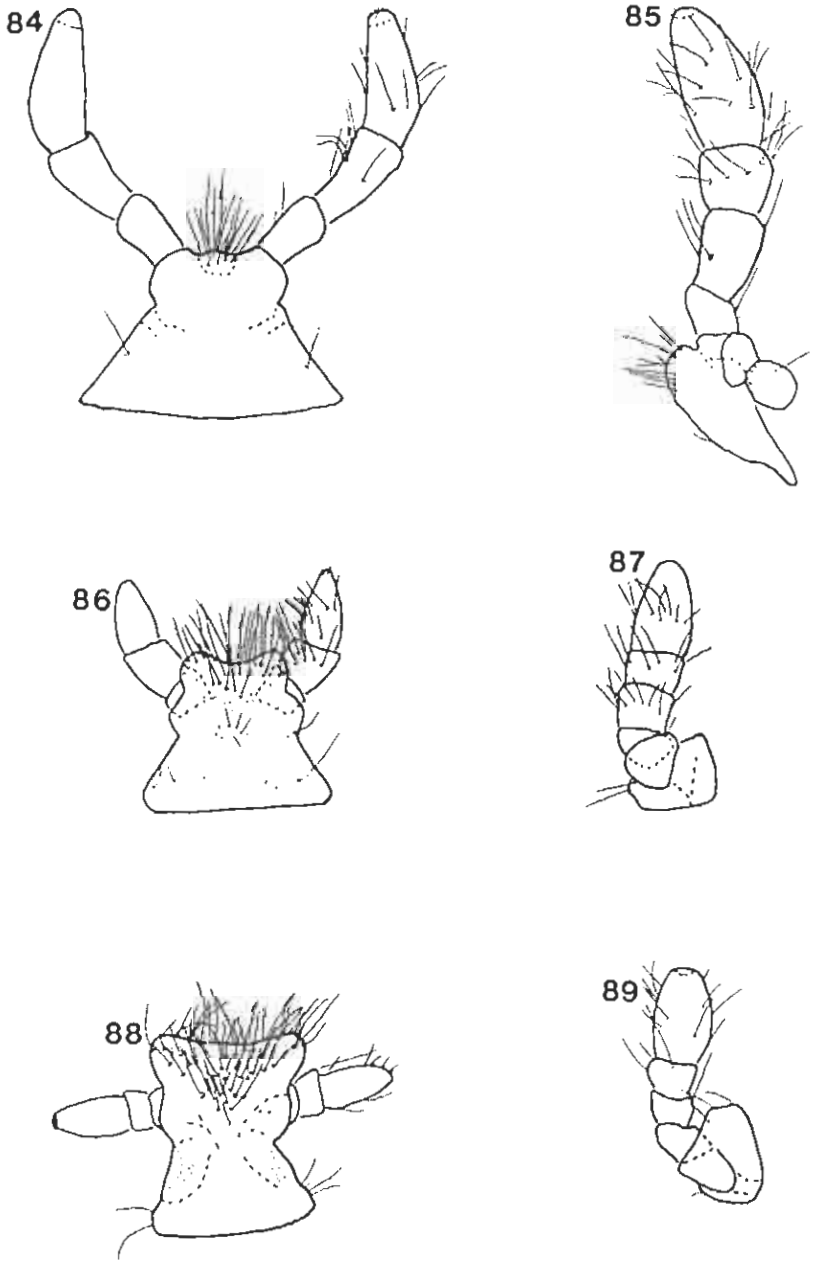
forms, subspecies applications were deemed inappropriate. It should be noted that the localities of selected illustrated body parts are for documentation only, and do not indicate morphological island types.

It was difficult to determine if the widely disjunct series described as *M. rhizophorae* is truly conspecific with *M. necydalea*, without available samples between the type locality of Belize and other areas of Mexico. *Methia rhizophorae* is defined on the basis of highly variable characters of coloration, width of the dorsal and ventral eye lobe connection, and often variable head punctation. These defining characteristics, including the distinctive coloration of the female, have been observed in specimens from the West Indies and the United States. Considering the very plastic nature of *M. necydalea* and some other species of *Methia* examined during the course of this study, we believe it is reasonable to conclude that they are the same species.

A paratype of *M. pulchra*, from Cozumel, has a labium with short, relatively blunt, premental lobes. We can separate this population by no other character. Specimens of *M. necydalea* examined from the Bahamas and parts of eastern Mexico have lobe shapes very similar in form. For this reason, we feel it is reasonable to also place *M. pulchra* in synonymy.

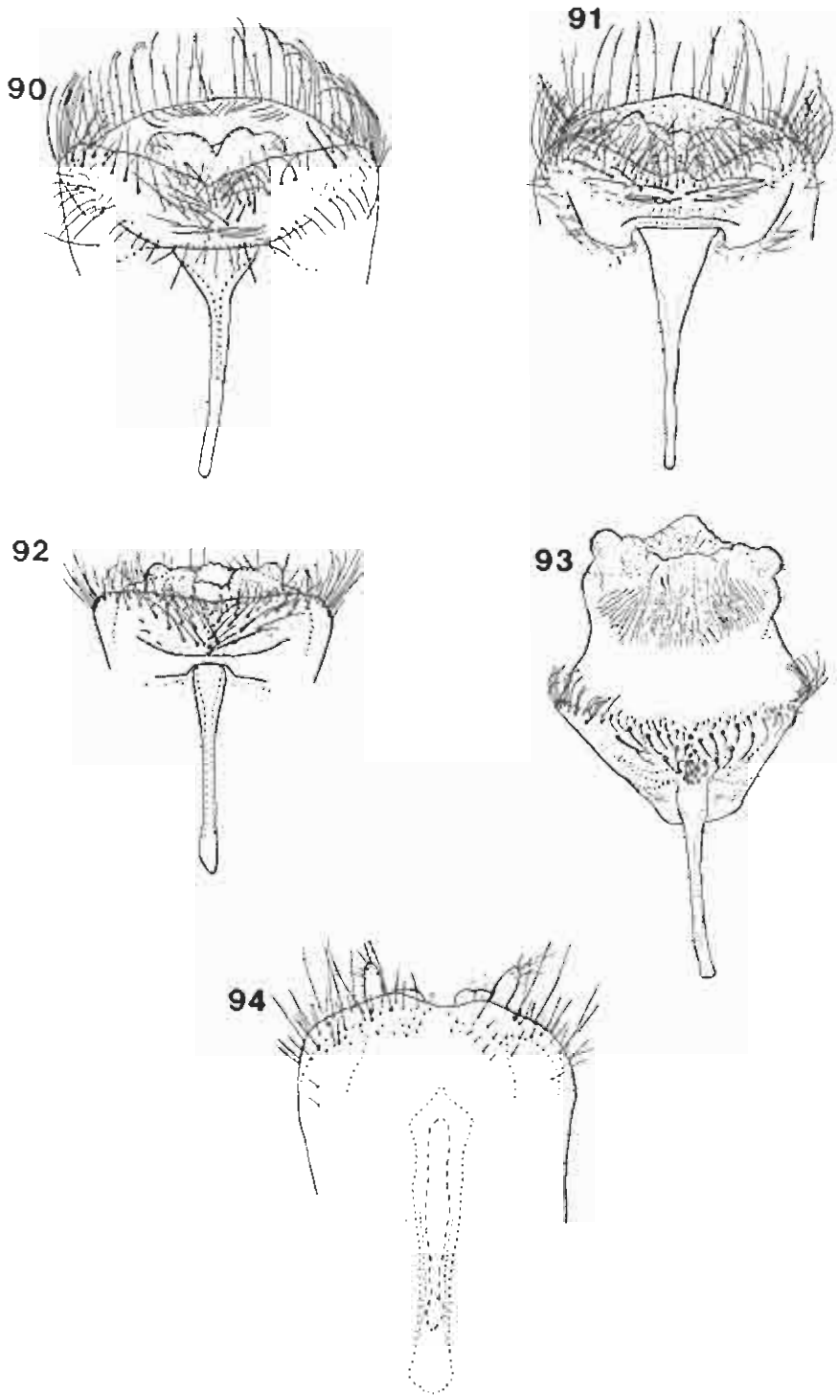
Although both these two latter synonymies are presently not as easy to defend as the others, due to the lack of specimens available from these regions of Mexico, the hypothesized taxonomy will be testable in the future when additional specimens become available.

The variability of *Methia necydalea* in the West Indies may be explained by its existence on a large number of islands, none of which have been isolat-



Figs 84-89. Labium (left) and maxilla (right): (84-85) *Styloxus bicolor*; (86-87) *Colcomethia xanthocollis*; (88-89) *Tessaropa tenuipes*.

ed for long enough to evolve unique, endemic species. Probably due to founder effects, intra-island variation is lower than inter-island variation, from areas which have adequate samples, most notably the Virgin Islands. Gene flow may continue between some of the islands although at slower



Figs 90-94. Female genitalia: (90) *Tessaropa tenuipes*; (91) *Coleomethia* sp. (new); (92) *Methia necydalea*; (93) *Methia jamaicensis*, extended; (94) *Styloxus bicolor*.

rates than would normally occur on a continuous land mass. This rate probably has not been constant due to eustatic changes altering the sizes of and distances between the islands. Islands which have become larger and simultaneously closer to adjacent land masses are likely to have higher rates of gene flow (MacArthur & Wilson 1967).

Although specimens from mainland regions exhibit relatively little variation compared to island populations, variation is relatively high in Florida. For example, there are two males and one female from southern Florida (Monroe and Dade Co.) which have a unique pronotal shape consisting of slight concavities dorso-laterally and a pronotal base extremely constricted (Fig. 21). There is another pair (one male and one female) from north-central Florida (Marion Co.) which have elytra unicolorous brown except for the apical 1/5 which is pale yellow brown (Fig. 68).

It is possible that more species of *Methia* exist in the West Indies than are recognized here. However, without more biological data, perhaps especially regarding host specificity, sibling species are impossible to morphologically differentiate. Confounding this host data though is the wide range of host species (gymnosperms and angiosperms) utilized by the more certain synonymies in this study (i.e., excluding *M. pulchra* and *M. rhizophorae*). Hence, host information may not be as informative as one would like. Regardless, we believe a more simplistic view is currently the best taxonomic estimate within this group.

Species *incertae sedis*

Methia taina Zayas

Methia taina Zayas, 1975: 53, fig. 6d. Chemsak & Linsley 1982: 12; Monné 1993: 28; Monné & Giesbert 1993: 30.

Tessaropa luctuosa Zayas

Tessaropa luctuosa Zayas, 1975: 54, fig. 7a. Chemsak & Linsley 1982: 13; Monné 1993: 31; Monné & Giesbert 1993: 31.

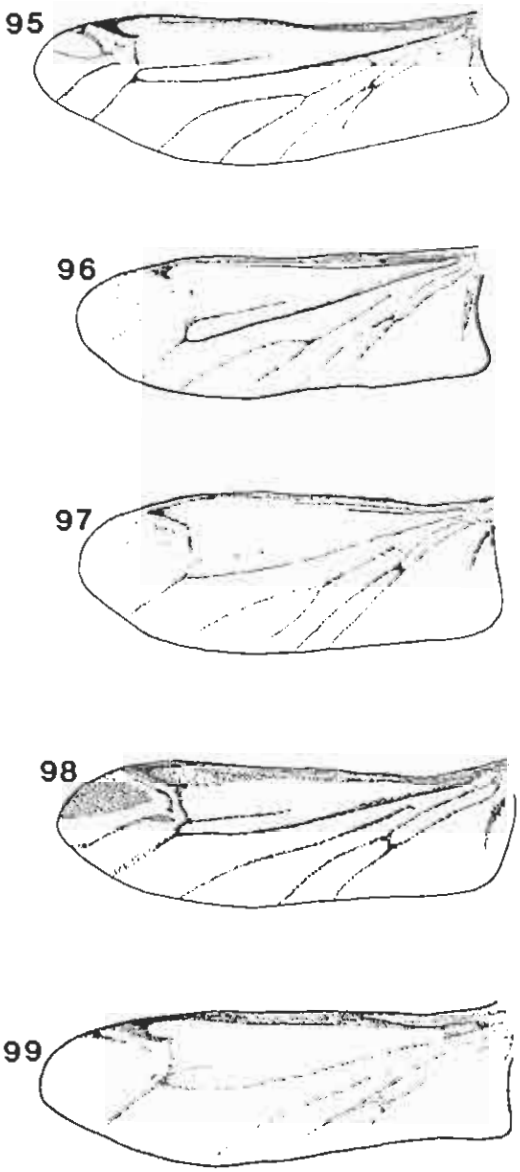
Discussion. – Both of these species were described from the eastern part of Cuba, the former from the Sierra Cristal and the latter from the Sierra Maestra. They were described from a single specimen each, deposited in the Zayas collection in Havana. M.A.I. was able to examine the types at the home of T. de Zayas Revuelta, but without a microscope or adequate lighting. The holotype of *M. taina* is a female labeled Sierra Crystal, Las Mulas, 6-1959. That of *T. luctuosa* is a male labeled Brazon, Rio Yara, 8-1965. Both bear red type circles. [Note that the month is at variance with Zayas' (1975) published notes].

Under the conditions available, the correct generic placement could not be determined for either specimen. *Methia taina* is definitely not conspecific with either of the other two known West Indian *Methia* species, nor any other *Methia* we have seen. Its habitus is similar to females of *Coleomethia* from Mexico and Texas, but both antennae are broken, so it is unknown if it has the thickened apical antennomeres characteristic of this genus.

Tessaropa luctuosa may well belong to *Methia*, as the reduced second antennomere is specifically mentioned. However, the possibility exists that it belongs to *Coleomethia* which shares this same characteristic.

Not to be ignored is the chance that these specimens represent the two sexes of a *Coleomethia*. On the basis of gross habitus, this is a distinct possibility. Placement of males and females of *Coleomethia* in different genera has occurred before (Hovore 1987). The definitive test would be to check wing venation, which if pleisiomorphic with four anal veins, would verify one or both species as belonging to *Methia*. If the derived venation of three anal veins was found, a complete female of each of these possible species would greatly help determine the correct placement within either *Coleomethia* or *Tessaropa*.

Part of the difficulty of working with these three previously discussed genera is the great amount of sexual dimorphism that occurs within some species. Additionally, many of the characters which have been used to separate these three methiine genera have been found to overlap. For example, *Tessaropa* cannot be distinguished from *Methia* by upper and lower eye lobe separation. Similar to *Tessaropa*, both *M. lycoides* and *M. batesi* have their eye lobes joined only by a line without any connecting facets (Chemsak & Linsley 1971). Other characters of *Tessaropa* purported to distinguish this genus are the reduced palps, imbricated abdomen, short elytra with widely rounded apices, and an indistinct second antennal segment (Linsley 1962). Species of *Methia* that we have examined, including some undescribed mainland species, approach these same character states. *Coleomethia* has been defined on the basis of a combination of characters (Hovore 1987), but the only unique characteristic of this genus is the female



Figs 95-99. Wings: (95) *Styloxus bicolor*; (96) *Methia jamaicensis*; (97) *Methia necydalea*; (98) *Tessaropa tenuipes*; (99) *Coleomethia xanthocollis*.

antennae with distal antennomeres thickened. Even the strongly abbreviated male abdomen, while generally good in distinguishing *Coleomethia* from other methiines, does exhibit overlap between *Methia* and *C. australis* Hovore.

In summary, due to the difficulty of determining the status of the two Zayas species from Cuba, we have decided to forego placing them at present until closer examination of the type material is allowed or more material is made available from Cuba.

Cladistic analysis of the Methiini

Before describing *Cyanomethia*, it was necessary to establish its monophyly relative to all other methiine genera. To examine this question, and to determine the relationships among the methiine genera, sensu Martins & Carvalho (1984), a cladistic analysis was conducted. Representatives of all genera in the tribe were included except for *Paratessaropa*, because the unique type is missing and additional material is unavailable.

Although the genus *Pseudomethia* Linsley shares several characters of the Methiini (deeply emarginate eyes, reduced intercoxal process, and abbreviated elytra), it was not used in the analysis because of major morphological differences between it and the other five genera. These differences include a single, elongate, narrow, paramere lobe, thickened antennal segments, a short, third antennal segment, an angulate pronotum, a declivous head, and mandibles which point forward. There was some question as to whether this monotypic genus belonged to the Methiini (Linsley 1962) and its exclusion from the Methiini has been continued by Martins & Carvalho (1984) who have provisionally placed it in the Oemini.

Twenty-five characters (nos. 0-24) were used to construct a cladogram. Ingroup taxa include *Methia necydalea*, *M. jamaicensis*, *M. arizonica* Schaeffer, *Tessaropa tenuipes* Haldeman, *Coleomethia xanthocollis* (Knull), *Coleomethia* sp. n. (MAIC), *Styloxus bicolor* (Champlain & Knull), and *S. fulleri* (Horn). The closely related species *Oeme rigida* (Say) in the Oemini was used as the outgroup. A list of the states for each genus is given in Table 1.

Table 1. Observed states of characters (nos. 0-24) among the genera used in the analysis of the Methiini.

Oeme	00000	00000	00000	00000	00000
Styloxus	01100	00101	10000	10001	000??
Cyanomethia	11010	01010	01000	01101	010??
Coleomethia	11010	01010	00101	01111	111??
Tessaropa	11011	00010	00000	01101	11101
Methia	01000	11000	00000	00101	01011

ENTOMOLOGICAL SOCIETY OF AMERICA
9301 Annapolis Road, Lanham, MD 20706-3115
tel. (301) 731-4535 • fax (301) 731-4538
e-mail esa@entsoc.org • http://www.entsoc.org

Dr. Donald G. Cochran, Associate Editor
Annals of the Entomological Society of America
306 Olde Point Road
Hampstead, NC 28443

March 19, 1999

Dr. Wenhua Lu
The Conservation Agency
6 Swinburne Street
Jamestown, RI 02835

Dear Dr. Lu:

Your manuscript, A99-003, has been accepted for publication in the *Annals* today. Since you plan to sent the original figures to ESA separately, I have not forwarded any copies to them. In sending the figures, please note that this is MS # A99-003, not 033 as you typed on the MS. Also, on Fig. 1 you must locate island # 6

Sincerely yours,

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Wenhua Lu

The Conservation Agency

6 Swinburne Street

Jamestown, RI 02835

Tel.: 401 - 423 - 2652

Fax: 401 - 423 - 2396

Tumbling Flower Beetles (Coleoptera: Mordellidae) of the Virgin Islands with Descriptions of New Species

WENHUA LU [1] and MICHAEL A. IVIE [2]

1 The Conservation Agency, 6 Swinburne Street, Jamestown, RI 02835

2 Department of Entomology, Montana State University, Bozeman, MT 59717

Abstract Eight species of tumbling flower beetles in four genera (Coleoptera: Mordellidae) occur in the Virgin Islands: *Mordella atrata* Melsheimer, *M. summermanae* Ray, *Tolidomordella leucocephala* (Quedenfeldt) comb. nov., *T. basifulva* (Quedenfeldt) comb. nov., *Glipostenoda guana* sp. nov. (18°29'N, 64°34'W, Guana Island, British Virgin Islands), *Falsomordellistena danforthi* (Ray) comb. nov., *Mordellistena irfianorum* sp. nov. (18°19'N, 64°43'W, St. John, U. S. Virgin Islands), and *M. lineata* Ray. Males of *T. leucocephala* and females of *T. basifulva* are described for the first time, as are the male genitalia of *M. summermanae*, *T. leucocephala*, *T. basifulva*, *F. danforthi*, and *M. lineata*. Species of *Mordella*, *Tolidomordella*, and *Falsomordellistena* are new records from the Virgin Islands. Range extension of *M. summermanae* to Jamaica is reported. A key to the species is provided.

KEY WORDS Mordellidae, Virgin Islands, West Indies, tumbling flower beetles, genitalia

Most of the Virgin Islands, about a hundred isles, cays, and vegetated rocks, both British and American, lie on the Puerto Rico Bank and were united with Puerto Rico at glacial maxima (Lazell 1995). An American outlyer, St. Croix, with several small coastal cays, is on a separate bank and is often thought to be more closely allied biologically to the Lesser Antilles (Lazell 1972). We report known mordellid beetle faunas from the islands on both banks (Fig. 1).

In the West Indies (*sensu* Bond 1985, excluding continental shelf islands), *Glipa* and *Conalia* each had a species and *Mordella* had seven in Blackwelder (1945). In his work on Puerto Rico, Ray (1937) listed 14 species of *Mordellistena*. Ray (1939) added another West Indian species to that genus. With an original description by Champion (1896), there were a total of 16 species of *Mordellistena* in Blackwelder (1945) from the West Indies. Maklin (1875) described *Mordellistena marginicollis* from Brazil, and Ray (1937) implied its presence in Puerto Rico by including it in his key (Wolcott 1950). Blackwelder (1945) did not list *M. marginicollis* from the West Indies and we have no evidence that it exists on the Puerto Rico Bank.

There has been no previous systematic work on tumbling flower beetles of the Virgin Islands. *Mordellistena ferruginea* (non *Mordella ferruginea* Fabricius 1775 or 1801) and *M. lineata* Ray were the only mordellids recorded nominally and anecdotally from the Virgin Islands (Miskimen and Bond 1970, Lazell 1995). Among the seven *Mordella* species, *M. leucocephala* and *M. basifulva* were described by Quedenfeldt (1886). Since then, no one has applied these names to known populations (Wolcott 1950), not even in Ray's extensive work of 1939. However, Wolcott (1936) listed host plants for adults of both species and implied that specimens other than the types from Puerto Rico had been determined by E. A. Schwarz. We believe Quedenfeldt's description of *M. leucocephala* was based only on females and *M. basifulva* only on males. Here we describe the male of *M. leucocephala*. It is possible that the female of *M. basifulva* is represented by specimens from Puerto Rico. These species are placed in *Tolidomordella* in today's nomenclature (Ermisch 1949-50, Jackman 1991).

Fabricius named two species "*Mordella ferruginea*." The first, *Mordella ferruginea* F. (1775) was moved to *Rhipiphorus* by Fabricius (1801). The second, *Mordella ferruginea* F.

(1801) is based on a type in Copenhagen labeled Essequibo, which is in Guyana, South America. The type specimen differs from the Puerto Rico Bank specimens in being larger, in having metallic reflection on the head, in having the antenna serrate, and in having a longer and narrower tibia with 4 transverse lateral ridges (examined by the junior author). Therefore, we believe *Mordella ferruginea* F. (1801) is not conspecific with the form from the Puerto Rico Bank. However, beginning with Quedenfeldt (1886), the name "*Mordella ferruginea*," transferred to *Mordellistena*, was used consistently by most authors for the Puerto Rico Bank species described herein.

The South American form named *Mordella ferruginea* by Fabricius (1801) is a primary junior homonym of *Mordella ferruginea* F. (1775). The situation is further complicated by the description of a European species, *Glipostenoda ferruginea* Horak (1995), which may be a congener. A solution to this problem is beyond the scope of this work.

There are some Fabrician names that might originate from the Virgin Islands but are not included above: *Mordella vittata* F. (1801) was not listed in Blackwelder (1945) under Mordellidae. *Mordella bifasciata* F. (1801), *M. haemorrhoidalis* F. (1801), *M. hamata* F. (1801), and *M. marmorata* F. (1801) were retained in this genus by Blackwelder (1945).

Because some descriptions are either simplistic, or contain errors, or provide no genitalic information, we redescribe most species or add to existing descriptions, following the guidelines of Franciscolo (1957), with emphasis on the genitalia. Length of a species is given as a range between the smallest and the largest (eye sighted) specimens measured in lateral view from the front edge of the pronotum to the tip of the elytron in an unaltered specimen. Elytral width is the maximum width across both elytra. Eye color varies among specimens due to different preserving materials and light angles; apical setae of the middle and posterior legs, as well as ridges and carinae on the posterior legs, are always black or much darker than the dermal color. Therefore, we do not mention these traits throughout this paper. Tarsal ratios are the proportion of tarsomeres given from basal to apical segments and from anterior to posterior legs, respectively, but the legs are not scaled *inter se, contra* Franciscolo (1957). Observations using scanning

electronic microscope (SEM) and genitalic terminology follow that of Lu et al. (1997). We have deposited most specimens and the holotypes of *Glipostenoda guana* sp. nov. and *Mordellistena irfianorum* sp. nov. in the Department of Entomology, Montana State University (MTSU). Specimens that are in the senior author's collection (WL) will eventually go to the U. S. National Museum of Natural History (USNM), or the Museum of Comparative Zoology, Harvard (MCZ).

Key to Species of Mordellid Beetles from the Virgin Islands

1. Posterior tibia with only a subapical ridge on outer face parallel to apical ridge; no other ridge on posterior tarsus 2

Posterior tibia either with a fine carina along dorsal outer edge or some oblique lateral ridges on outer face other than the subapical ridge 3

2. Black, suboval, small, pygidium very short, flat at base .....

Mordella summermanae Ray

Black, cuneiform, large, pygidium twice as long as hypopygium .....

Mordella atrata Melsheimer

3. Posterior tibia with a fine carina along dorsal outer edge in addition to subapical ridge; such carina also indicated on basitarsus 4

Posterior tibia with some oblique ridges on outer face in addition to subapical ridge; such oblique ridges also indicated on tarsal segments 5

4. Female head and a semicircular spot on anterior pronotum yellow, elytron with two small anterior yellow spots and one large posterior yellow spot; male black with one large yellow spot on elytron before middle, another behind middle .....

Tolidomordella leucocephala (Quedenfeldt) comb. nov.

Female head yellow, elytron with two small anterior yellow spots and one large posterior yellow spot; male black with a ferruginous humeral vitta covering the two small anterior yellow spots but not the large posterior yellow spot .....

Tolidomordella basifulva (Quedenfeldt) comb. nov.

5. Head and pronotum black 6

Derm generally ferruginous, at least pronotum so 7

6. Elytron black; two ridges on outer face of posterior tibia other than the subapical one; two each on basal and second segments of posterior tarsus .....

Mordellistena irfianorum sp. nov.

Elytron with a flavous stripe running from base to apex, leaving suture and margin black; two ridges on outer face of posterior tibia other than the subapical one; two on first segment, one on second segment of posterior tarsus .....

Mordellistena lineata Ray

7. Head sometimes fuscous, otherwise totally ferruginous, including antenna .....

Glipostenoda guana sp. nov.

Head and thorax flavous; elytron fuscous with a flavous vitta at base, tapering caudad; at least seven apical segments of antenna fuscous .....

Falsomordellistena danforthi (Ray) comb. nov.

1. *Mordella atrata* Melsheimer

Mordella scutellaris F. Leng and Mutchler 1917, Ray 1939, Blackwelder 1945 (non Fabricius 1801).

Mordella atrata Melsheimer, 1846; Liljeblad 1945.

Type Locality. Pennsylvania, USA.

Type. Not listed (Bright 1986). Ray (1939) used *M. scutellaris* F. (1801) for this species from Puerto Rico; Liljeblad (1945) pointed out that *M. scutellaris* was originally described as bicolored, and *atrata* was the oldest available name for the black mordellid otherwise resembling *scutellaris*. We compared our material with MCZ specimens determined by Liljeblad and follow Liljeblad (1945).

Length: 3.2-4 mm. Cuneiform, more robust in female than in male. Derm entirely black, often iridescent under light; pubescence on upper surface brownish, on scutellum cinereous; underside and basal pygidium with longer cinereous hairs.

Liljeblad (1945) has adequately redescribed the species except for the following characters: Middle tibia as long as its tarsus; penultimate segments of anterior and middle tarsi slightly enlarged and notched at apex. Posterior tibia with a short subapical ridge, parallel to apical margin, no continuous dorsal carina but with small granules scattered in an irregular line on dorsum; the same dorsal granules weakly indicated on basitarsus, much less so on second segment of posterior tarsus. Outer spur of posterior tibia 1/3 (female) or 1/4 (male) shorter than inner one. Tarsal ratios: 4-2-2-3-5, 3-2-2-4-8, 2-2-3-6. Pygidium long and stout, twice as long as hypopygium; hypopygium about twice as long as penultimate segments. Urosternites and genitalia as in Lu et al. (1997).

Previous Records. Cuba (Leng and Mutchler 1917), Puerto Rico, North, Central, and South Americas (Blackwelder 1945).

Material Examined. BRITISH VIRGIN ISLANDS: Guana, Quail Dove Ghut, 600 ft., 1, 20-25.iv.1993, flight intercept trap, W. P. Liao; Guana, 3, 10.x.1994, on sea grape blossoms, *Coccoloba uvifera*, W. Lu (MTSU); Guana, Muskmelon Bay, 1, 5.x.1995, sweeping on *Lantana involucrata*, W. Lu (WL).

Remarks. Champion (1889) and Liljeblad (1945) both mentioned that the third segment of the antenna was a little longer than the fourth. We find that the two segments are of the same length. They did not mention the granules on the dorsum of the posterior tibia. All North American specimens in USNM and MCZ examined by the senior author have these granules.

Ray (1939) reported five *M. scutellaris* from Puerto Rico. The senior author was able to locate and examine these five specimens at USNM. Although Blackwelder (1945) made *atrata* a synonym of *scutellaris*, Ray's specimens are totally black instead of bicolored as in *scutellaris sensu stricto*. Despite the fact that many early workers called the all-black form *scutellaris*, most authors today accept Liljeblad's arrangement and so do we.

2. *Mordella summermanae* Ray

(Fig. 3 and 10A-C)

Mordella summermanae Ray, 1939.

Type Locality. Constanza, Dominican Republic.

Holotype. A unique female, 22.v.1927, A. Wetmore; USNM 52928. We could not locate this specimen, but we compared our material with specimens from the Dominican Republic that fundamentally fit Ray's (1939) description.

Length: 1.7-2.2 mm. Form short, suboval, elongate, broadest near base of pronotum. Derm fuscous to black, spurs of posterior tibia flavous; basal four segments of antenna less so; apical segments of antenna and legs (except for posterior tibia) fuscous. Upper surface covered with yellowish brown pubescence, hairs of underside cinereous.

Head big, as broad as pronotum; eye oval (pear-shaped, narrower anteriorly), reaching occiput, finely granulated with sparse short hairs; distance between eyes on vertex wider than two eyes combined. Antenna shorter than head and pronotum combined, scarcely reaching base of pronotum; segments 1 and 2 subequal, 3 and 4 subequal, shorter and narrower; 5 triangular, 1/3 longer than 4, and three times as broad at apex; 6-10 strongly serrate, twice as broad as long, each slightly shorter than 5; 11 rounded to apex, a little longer than 10. Distal segment of maxillary palpus isosceles triangular with outer side longer, almost equilateral in males.

Pronotum broader than long, widest subbasally, sides parallel; basal angles almost reticulate angles, base arcuate, basal lobe short, but broadly rounded. Scutellum very small, broadly triangular, apical angle rounded. Elytra about twice as long as broad, widest subbasally, attenuate apically; apices individually rounded with fine but distinct margin.

Middle tibia slightly longer than its tarsus or as long; penultimate segments of anterior and middle tarsi slightly enlarged and notched at apex. Posterior tibia with a short subapical ridge, parallel to apical margin. Outer spur of posterior tibia 1/3 as long as inner one. Tarsal ratios: 3-1-1-2-4, 3-1-2-3-8, 2-2-3-6.

Pygidium flat, short, but a quarter longer than hypopygium, very broad at base, but 1/3 longer than broad in dorsal view; sides straight, apex truncate; hypopygium 1.5-2 penultimate segments. Urosternites equal in length; furca twice as long as tube, tube as long as paramera, furca one and a half as long as epimere; epimere wide and elliptical, twice as long as left

parameron or one and a half as long as right parameron; penis about 4.5 as long as epimere with a simple pointed tip.

Left parameron (Fig. 10B) short and flattened with a medial branch (Lu et al. 1997) apically; a dent at base of medial branch (Fig. 10A). Right parameron typical of type B (Fig. 10C) with an insignificant basal ridge (Lu et al. 1997); its ventral branch extremely long and thickened from base on, comparable to those of *Glipa* and *Hoshihananomia* (Lu et al. 1997), with a small prong (Fig. 10C, arrow).

Previous Records. Dominican Republic: Constanza (Ray 1939).

Material Examined. U. S. VIRGIN ISLANDS: St. Thomas, Est. Nazareth, 1, 27.vii.-19.x.1994, 40 ft. flight intercept trap, M. A. and L. L. Ivie (MTSU). BRITISH VIRGIN ISLANDS: Guana, 8, 2-10.x.1994, sweeping on sea grape blossoms, *Coccoloba uvifera*, W. Lu (MTSU). JAMAICA: St. Catherine Parish, Little Goat Island, 5, 1.iii.1995, W. Lu; Trelawny Parish, Good Hope, 1, 4.iii.1995, sweeping on composite blossoms, W. Lu; Manchester Parish, 2.25 mi. northwest Mandeville, Marshall's Pen, 2, 26.ii.1995, W. Lu (WL). DOMINICAN REPUBLIC: Peravie, 17 km east San Jose de Ocoa, 1, 8.viii.1979, G. B. Marshall; Peravie, 21 km northwest San Jose de Ocoa, 1, 9.viii.1979, C. W. O'Brien (MTSU).

Remarks. In Ray's (1939) description the lighter color of the basal four segments of the antenna was not mentioned, and the width of segments 5-10 were said to be only "as broad as long." We have also observed that the frons, the mouthparts except the tip of the mandibles, and the anterior femur are often flavous. The right parameron embraces the left one, its small prong of the ventral branch articulates with the dent at the base of the medial branch of the left parameron.

The species is not often collected, but is occasionally numerous. This is the first record of it from the Virgin Islands and Jamaica.

3. *Tolidomordella leucocephala* (Quedenfeldt) comb. nov.

(Fig. 4 and 10D-F)

Mordella leucocephala Quedenfeldt, 1886.

Type Locality. 18°29'N, 64°34'W, Guana Island, British Virgin Islands.

Neotype. Quedenfeldt (1886) did not give any locality for his specimens and stated that the specimen given to him by C. Krug did not have locality data. His material was given to Obenthur who might have deposited it in France or Germany . Curators in the Humboldt Museum, Berlin, and the National Museum of Natural History, Paris, have not been able to locate his specimens. Because he described only the female and the male characters are usually more important in identification for this group of beetles, we herein designate a male as the neotype, collected by W. Lu, 5.x.1996, on Guana Island, and deposited in MTSU.

Length: 1.9-2.7 mm. Form elongate, subparallel, broadest before base of pronotum. Male derm castaneous to black with frons, antenna, palpus, legs, and often apical pygidium fulvous; elytron with two large and transverse yellow spots: one occupying most of the basal third of elytron, almost reaching base, the other behind middle; both spots not reaching sutural and side margins. Female head and a semicircle on anterior pronotum light yellow, leaving pronotum a large black basal margin; elytron with two small anterior yellow spots before middle: one round, near suture a little below base, the other transverse, lower down close to side margin; elytron with another large posterior yellow spot behind middle: transverse and oblong, not reaching suture but often touching side margin. Surface covered with pubescence partaking distinctly of ground colors.

Head small, slightly narrower than pronotum; eye oval, reaching occiput, moderately granulated with dense setae-like hairs. Antenna shorter than head and pronotum combined, not reaching base of pronotum; segment 3 distinctly small, triangular, not much longer than broad, 4 about 1/3 wider at apex and slightly longer than 3; segments 5-7 subserrate, slightly increasing in width and length, 5 twice as long and broad as 3; 8-10 subequal, each as long as 7 and 1/3 longer than broad; 11 suboval, 1/3 longer and slightly broader in middle than 10. Distal segment of maxillary palpus boat-shaped or hammer-shaped in male, with apical side much less sclerotized; scalene triangular in female with outer side longer and rounded, apical side slightly shorter than inner side.

Pronotum 1/3 broader than long, widest in middle, evenly rounded to apex; basal angles obtuse, base arcuate, basal lobe broadly rounded. Scutellum small, triangular, rounded at apex. Elytra at least twice as long as broad, slightly narrower at base than pronotum, subparallel on basal two thirds, then attenuate apically; apices individually rounded with fine but distinct margin.

Middle tibia as long as its basal four tarsal segments; penultimate segments of anterior and middle tarsi bilobed. In addition to a subapical ridge halfway across outer face and parallel to apical ridge, posterior tibia with a fine carina along dorsal outer edge, interrupted halfway to genu; another such carina, but more than halfway along dorsal outer edge on basitarsus. Outer spur of posterior tibia very short, 1/5 as long as inner one. Tarsal ratios: 2-1-1-1-4, 2-1-1-3-8, 3-4-5-10.

Pygidium conical, stout at basal two thirds, then sharply attenuate to apex, curved down a little from side view, 2.5 as long as hypopygium. Eighth sternite with a median protuberance long and rounded at apex, and a lateral lobe on each side; ninth sternite slender, with apical portion enlarged. Epimere 1.5 as long as paramera, furca as long as tube, with furcal arms strongly thickened and hooked apically. Penis short, as long as pygidium, twice as long as epimere; its apical first third greatly flattened and enlarged, terminating in a round fleshy lobe.

Left parameron (Fig. 10D) bearing a highly developed and flap-like dorsal branch with setae all over inner surface, and a bare, blunt, and strongly sclerotized medial branch (Lu et al. 1997); inner surfaces of dorsal and medial branches normal to each other instead of in the same plane. Right parameron (Fig. 10E) bearing a dorsal branch highly developed, long, and flap-like with setae all over the inner surface, and a short, bare, truncate, strongly sclerotized ventral branch; basal angle of ventral branch with a sharp and long extension (Fig. 10E and F, arrows); no setae on the outer surface (Fig. 10F).

Previous Records. Probably Puerto Rico (Quedenfeldt 1886) because the specimen's donor, C. Krug, was a resident there and Wolcott (1950) implied that the types were collected by J. Gundlach there. Puerto Rico (Leng and Mutchler 1914, Wolcott 1936).

Material Examined. Male: U. S. VIRGIN ISLANDS: St. John, Lameshur Bay, 1, iii.1984, malaise trap, M. B. Muchmore; St. John, Lameshur Bay, 1, 21-28.vii1994, ultraviolet light trap, M. S. Becker (MTSU). St. Thomas, East Botany Bay; 1, 29.vii-15.x.1994, M. A. and L. L. Ivie (MTSU). BRITISH VIRGIN ISLANDS: Necker, 1, 22-25.vii.1988, C. O'Connell (MTSU). Guana (in addition to neotype) -- Sugarloaf Trail, 100-800 ft., 1, 9.x.1994, M. A. and L. L. Ivie; 0-80 m, 1, 10-25.vii.1988, S. E. Miller and C. O'Connell; 3, 1-14.vii.1984, S. E. Miller and P. M. Miller; 1, 16.x.1993, C. Bartlett and J. Cryan; 1, 19.x.1993, malaise trap, C. Bartlett and J. Cryan; 1, 18-19.x.1993, C. Bartlett and J. Cryan; 3, 10.x.1994, W. Lu; North Beach, 1, 11-16.x1992, malaise trap, R. R. Snelling; plantation area, malaise trap, 2, 16-20.x.1992, R. R. Snelling (MTSU); Iguana Trail, 2, 4.x.1996, W. Lu; Liao Weiping Trail, 7, 5.x.1996, W. Lu; Guail Dove Ghut, 2, 7.x.1996, W. Lu; Long Man's Point, 1 9.x.1996, W. Lu; Lower Iguana Trail, 2, 12.x.1996, W. Lu; Pyramid, 2, 13.x.1996, W. Lu (WL). PUERTO RICO: Ponce, Torres Finca, 1, 24.viii.1933, *Ocotea* sp., R. G. Oakley (USNM).

Female: BRITISH VIRGIN ISLANDS: Guana -- 1, 1-14.vii.1984, S. E. and P. M. Miller; Bigelow Road, 1, 17-vii.1994, at night, S. A. Bucklin (MTSU); Liao Weiping Trail, 2, 5.x.1996, W. Lu; Iguana Trail, 1, 6.x.1996, W. Lu; Quail Dove Ghut, 3, 7.x.1996, W. Lu; Long Man's Point, 1, 9.x.1996, W. Lu; Lower Iguana Trail, 1, 12.x.1996, W. Lu (WL). Great Camanoe, 2, 12.x.1996, W. Lu (WL).

Remarks. The colors of the head and thorax in the male can vary from fulvous to black, as can abdominal segments and legs in both sexes. The senior author has examined and compared specimens totally fulvous, totally black, and intermediates. There are no differences in male genitalia and wing venation. We believe the difference in dermal color is because of age of the live animals. The elytral yellow spots of the male (Fig. 4) are about equal in size; the one posterior to the middle is as long as or slightly longer than the last apical portion of the elytron; the black band between the two yellow spots is at least as long as or longer than any other black band and a yellow spot combined. The head and a semicircle on the anterior pronotum are

sometimes flavous in the male. This form is scarce but recorded from the islands of St. John, St. Thomas, Guana, and Great Camanoe.

Most specimens collected by the senior author during 1996 were on blossoms of pigeonberry, *Bourreria succulenta* (Boraginaceae), fiddlewood, *Citharexylum fruticosum* (Verbenaceae), and on leaves of dogwood, *Piscidia carthagenensis* (Leguminosae). A few were on blossoms of yellow cedar, *Tecoma stans* (Bignoniaceae) and tourist tree, *Bursera simaruba* (Burseraceae).

T. leucocephala closely resembles *T. discoidea flaviventris* (Smith) from Florida and Texas in the male genitalia, wing venation, and male elytral pattern. However, *T. d. flaviventris* is not sexually dimorphic like *T. leucocephala*, and sometimes has a flavous humeral dash on the elytron, and the basal angle of the ventral branch of the right parameron does not have the sharp and pointed extension (Lu et al. 1997) of male *T. leucocephala*. Because the basal angle extension, the base of the right parameron of *T. leucocephala* is very wide (Fig. 10E and F).

4. *Tolidomordella basifulva* (Quedenfeldt) comb. nov.

(Fig. 5)

Mordella basifulva Quedenfeldt, 1886.

Type Locality. 18°00'N, 66°37'W, Ponce, Puerto Rico.

Neotype. Quedenfeldt (1886) did not give any locality for his specimens. Wolcott (1950) implied that the types were collected by J. Gundlach in Puerto Rico. Because we could not locate Quedenfeldt's specimens, for reasons noted above, we herein designate a male as the neotype, collected by R. G. Oakley, 11.ix.1933, Ponce, Torres Finca, on *Ficus*, and deposited in USNM.

Length as in *T. leucocephala* but slightly narrower. Male similar to female *T. leucocephala* except for the following: Head fulvous with a dark cloud on vertex; pronotum with a large black spot on disc leaving marginal edges fulvous; elytral color various from fulvous to black, a wide humeral vitta fulvous all the way towards elytral suture, at least half way down the elytron, overwhelming the two small anterior yellow spots in the same location as in female *T. leucocephala*; basal four segments

of antenna, underside of thorax, and legs lighter than elytra, from flavous to fulvous. Distal segment of maxillary palpus boat-shaped.

Median protuberance of eighth sternite long and pointed; ninth sternite elongate, with apical portion enlarged and strongly asymmetrical. Epimere twice as long as paramera, furca twice as long as tube, with furcal arms hooked but not thickened. Penis long, three times as long as epimere; its basal second quarter slightly enlarged, but apical first quarter greatly enlarged, apical termination as in *T. leucocephala*.

Paramera similar to those of *T. discoidea flaviventris* (Lu et al. 1997); for right parameron, its ventral branch shorter than that of *T. leucocephala*, with a basal angle sharp but no extended root as in *T. leucocephala*; middle of dorsal branch of right parameron with some very short setae.

Previous Records. Puerto Rico (Quedenfeldt 1886, Leng and Mutchler 1914, Wolcott 1936).

Material Examined. U. S. VIRGIN ISLANDS: St. John, Estate Caneel Bay, Lind Point, 1, 2.i.1993, leaf litter (MTSU). BRITISH VIRGIN ISLANDS: Guana, Quail Dove Ghut, 1 male, 7.x.1996, *Acacia*, W. Lu (WL). Tortola, Sage Mountain, 450 m, 2 males, 4.x.1996, W. Lu (WL). PUERTO RICO (in addition to neotype): Mayaguez, 1 male, 21.vii.1933, coffee leaf, no collector, but the handwriting is R. G. Oakley's (USNM).

Remarks. All specimens of this type are males. Quedenfeldt (1886) did not mention the sex of his specimens but apparently named *T. basifulva* based on male specimens only. The fulvous humeral vitta on the elytron is so strong that the two anterior small yellow spots are sometimes merely suggestive. Four specimens from Puerto Rico -- Ponce, 1, 11.ix.1933, *Ficus*, R. G. Oakley; Ponce, R. B. Noise F., 1, 12.i.1933, coffee, R. G. Oakley (USNM); Naricao Forest Reserve, 1, 26.vii.1979, G. B. Marshall (MTSU); Maricao Forest, 2-3,000 ft., 1, 30.v-2.vi.1938, Darlington (MCZ) -- have a yellow head as in female *T. leucocephala*, but the pronotum is entirely black, missing the anterior yellow semicircle characteristic of female *T. leucocephala*. The elytra are similar to those of female *T. leucocephala*. All specimens of this form are females; one of them was collected in the same locality, on the same date, on the same host plant, and by the same collector as the neotype. We thus believe that this form may be the female of *T.*

basifulva. It appears that in the Virgin Islands *T. basifulva* is outnumbered by *T. leucocephala* and thus it is not surprising that we have not collected female specimens of *T. basifulva* there.

5. *Glipostenoda guana* sp. nov.

(Fig. 6 and 10G-I)

Mordellistena ferruginea F. Quedenfeldt 1886; Leng and Mutchler 1914, 1917; Wolcott 1936, 1950 (non *Mordella ferruginea* Fabricius 1775 or 1801).

Mordellistena ferruginea (F.). Ray 1937, Miskimen and Bond 1970, Lazell 1995 (non *Mordella ferruginea* Fabricius 1775 or 1801).

Length: 2.1-3.3 mm. Form elongate, narrow, sides subparallel, attenuate and rounded gradually caudad from apical quarter of elytra. Derm ferruginous; head and pronotum sometimes with fuscous clouds; basal segments of antenna, maxillary palpus, anterior and middle legs lighter (flavoferruginous), underside darker. Surface covered with fine pubescence partaking of ground color.

Head small and convex; eye large, hairy, and coarsely granulated, reaching occiput, emarginate behind antenna; eye width greater than its length, distance between eyes on vertex less than 2 eyes combined. Antenna filiform and long, antennal segments of males more slender than those of females, longer beyond base of pronotum, segment 5 shorter than 3 and 4 combined, segments 5-10 slightly decreasing in length and increasing in width, each segment ranging 2.5-2 times as long as broad in sequence. Antennal segments of females more stout, segment 5 as long as 3 and 4 combined, 5-10 obviously decreasing in length and increasing in width, each segment ranging 2-1 times as long as broad in sequence. Segment 11 slightly longer than 10, sides straight, apex rounded. Distal segment of maxillary palpus scalene triangular, inner side a little longer than apical side and shorter than outer side, apical side and angle rounded.

Pronotum a little broader than long, broadest at base; basal angles barely obtuse or nearly rectilinear, base arcuate, basal lobe short and broadly rounded. Scutellum triangular, sides straight, apical angle rounded. Elytra at least 2.5 times as long as broad, sides subparallel on basal

three quarters, thence broadly rounded to apex; apices individually rounded. Metasternal plate with a transverse suture (TSM, Franciscolo 1962).

Middle tibia as long as its tarsus; penultimate segments of anterior and middle tarsi enlarged and emarginate at apex. In addition to a short subapical ridge, posterior tibia with two long oblique ridges, extending halfway across outer surface; basitarsus with three, second tarsal segment with two, short oblique ridges; basal ridge on basitarsus sometimes rudimentary. Outer spur of posterior tibia a quarter length of inner one. Tarsal ratios: 1-1-2-3-6, 1-1-2-3-6, 3-3-4-8.

Pygidium long, at least 2.5 as long as hypopygium in male, slightly shorter in female, conical, slender, and attenuate to apex. A small area in median protuberance of eighth sternite without setae, and a large area in basal two third of eighth sternite less sclerotized; tube of phallobase short, as long as right parameron, furca longer than epimere; thus phallobase as long as paramera and epimere combined; epimere twice as long as right paramera. Penis slightly more than three times as long as epimere, and terminating in a simple lobe with a lateral flange (Fig. 10G, arrow) on each side.

Paramera typical of type D (Franciscolo 1957): mitten-like and more or less symmetric by branching dorso-ventrally. Dorsal branch of left parameron strongly sclerotized, thickened and triangular in apical cross section, longer by half than ventral branch, which is thin, sharp, bare, but sclerotized (Fig. 10H); basal prominence of dorsal branch blunt (Fig. 10H). Right parameron shorter and stouter than left, branching from basal 1/2 with a flap-like dorsal branch and a ventral branch shorter, bare, but strongly sclerotized (Fig. 10I).

Previous Records (as *Mordellistena ferruginea*). Puerto Rico (Quedenfeldt 1886, Leng and Mutchler 1914, Ray 1937). U. S. Virgin Islands: St. Thomas (Quedenfeldt 1886, Leng and Mutchler 1914, Wolcott 1950, Blackwelder 1945), St. Croix (Miskimen and Bond 1970). British Virgin Islands: Necker (Lazell 1995). A record for U. S. (Blackwelder 1945) has no known source. Quedenfeldt (1886) mentioned specimens from Columbia, South America.

Material Examined. We have collected and examined numerous specimens (now in MTSU + WL) from the Virgin Islands and only give island records (number of specimens) as follows. U.

S. VIRGIN ISLANDS: St. Croix (8), St. John (37), St. Thomas (15). BRITISH VIRGIN ISLANDS: Guana (55+63), Jost Van Dyke (4), Necker (7+15), Virgin Gorda (4+2), Great Dog (+1), George Dog (+2), Great Camanoe (+19), Scrub Island (+1). PUERTO RICO: Ponce, 1 male, 1933-34, R. B. Oakley; Guanica, 1 female, 25.ix.1947, Caldwell; Rincon, 3, 1963, J. Maldonado; Rincon, 3, iv.1964, J. Maldonado (USNM); Mona Island, 7-13.xi.1992, 1, Snelling and Torres; Pico Atalaya, 1, 3.vii.1958, M. W. Sanderson; Guanica Forest Reserve, 1, 26.ix.1987, M. A. Ivie; Hwy. 371, 10 km, 25.vii.1979, G. B. Marshall; Maricao Forest Reserve, 1, 26.vii.1979, G. B. Marshall; Abajo Forest Reserve, 1, 27.vii.1979, G. B. Marshall; Guajataca Forest Reserve, 2, 27.vii.1979, G. B. Marshall; Toro Negro, 1, 22.vii.1979, C. W. O'Brien et al.; Maricao Forest Reserve, 1, 25.vii.1979, B. O. O'Brien; Maricao Forest Reserve, 1, 26.vii.1979, B. O. O'Brien; Rio Abajo Forest Reserve, 24.vii.1979, B. O. O'Brien; Maricao Forest Reserve, 2, 25.vii.1979, C. W. O'Brien (MTSU).

Type Locality. 18°29'N, 64°34'W, Guana Island, British Virgin Islands.

Holotype. Male, collected by W. Lu, 10.x.1996, on Guana Island, and deposited in MTSU.

Paratypes. The remaining 54 MTSU specimens listed above from Guana Island.

Etymology. Named for Guana Island as a noun in apposition.

Remarks. This is a very abundant species, can be found on blossoms of *Lantana*, *Acacia*, *Citharexylum fruticosum*, and various leguminous plants. The ridges on the posterior tibia and tarsus vary among individuals. An extremely small individual from St. John has only one long oblique ridge on the posterior tibia, in addition to the short subapical one; it has only two ridges on the basitarsus and one on the second segment of the right tarsus, and a rudimentary second on the second segment of the left tarsus. The posterior tibia and basitarsus rarely show a rudimentary 4th ridge. The ferruginous color in this specimen and other small specimens collected on Guana and Virgin Gorda is so pale that it appears almost yellow. Newly emerged adults also are pale.

All four specimens from Jost Van Dyke are entirely black-headed. Their antennal segments 3 and 4 are short and narrow so that 5 is as long as 3 and 4 combined. Similar

individuals were collected on St. John and Guana. There is a range of color variation on the head from flavoferruginous, fuscous, to entirely black, all with the same type of antennae, on the latter two islands. We observed no difference in the male genitalia and regard this color form on Jost Van Dyke as interisland variation.

6. *Falsomordellistena danforthi* (Ray) comb. nov.

(Fig. 7.)

Mordellistena danforthi Ray, 1937; Wolcott 1950.

Type Locality. Villalba, Puerto Rico.

Holotype. Male, 21.vi.1934, C. M. Matos; USNM 51599. We examined both the holotype and allotype.

Length: 2.0-2.8 mm. Form elongate, sides subparallel. Derm flavous; elytron fuscous with a flavous, broad, humeral spot along base to suture, narrowing caudad to basal 1/3 of elytron; eye, apical seven segments of antenna, posterior ventral abdominal segments, and pygidium fuscous. Surface densely covered with fine golden pubescence.

Ray (1937) has adequately described the species except for the following characters: Metasternal plate without TSM. Middle tibia as long as its basal four tarsal segments; penultimate segments of anterior and middle tarsi enlarged and slightly emarginate at apex. In addition to a short subapical ridge, posterior tibia with two long oblique ridges, extending halfway across outer surface; posterior basitarsus with three, second segment with two, short oblique ridges; basal ridge on basitarsus sometimes rudimentary. Outer spur of posterior tibia 1/4 as long as inner one. Tarsal ratios: 2-1-2-3-4, 3-2-3-4-9, 3-4-5-9.

Pygidium long, 2.5-3 times as long as hypopygium, shorter in females, conical, slender, and attenuate to apex. Median protuberance of eighth sternite appearing bifurcate due to setae and a less sclerotized area all the way to base, ninth sternite twice as long as eighth; furca twice as long as tube or paramera, and as long as epimere; epimere twice as long as right parameron; ventral branch of left parameron extremely narrow and pointed, basal prominence set off its dorsal

branch by a split. Penis four times as long as epimere with a simple pointed tip, apical first and third quarters enlarged with a constriction on apical second quarter.

Previous Records. Puerto Rico (Ray 1937, Wolcott 1950).

Material Examined. U. S. VIRGIN ISLANDS: Great St. James, 1, 20.x.1994, M. A. Ivie (MTSU). St. John, 2, 15.vii.1994, beating at night, M. S. Becker; St. John, 1, 21-28.vii.1994, ultraviolet light, M. S. Becker (MTSU). BRITISH VIRGIN ISLANDS: Virgin Gorda, 1, 14.iv.1956, J. F. Clarke (USNM). Prickly Pear Island, 1, 6.iv.1958, J. F. Clarke (USNM). Guana, 1, 1-14.vii.1984, S. E. and P. M. Miller; 5, 4-10.x.1994, W. Lu (MTSU). Necker, 4, 30.ix.1996, *Citharexylum fruticosum*, W. Lu (WL). George Dog, 1 female, 30.ix.1996, *Lantana*, W. Lu (WL).

Remarks. One specimen from St. John (MTSU) has an additional rudimentary ridge on both the posterior tibia and the basitarsus. According to Ray (1937), the scutellum, apical two thirds of the pygidium, and only three abdominal ventral segments were fuscous, but he also stated that "the abdominal segments of the female (except pygidium) lack the fuscous coloration of the male, and the general castaneous color is lighter." We have observed variation in the abdominal ventral segments from totally fuscous to totally flavocastaneous. The pygidium may be as he described or totally fuscous. We see no variation in the color of the scutellum, which is as flavous as the front part of the body or the humeral spots on the elytra. Ray (1937) described the eyes as "emarginate behind antennae." We find the eye is in fact almost rounded, but tapers acutely towards the antennal base; the width and length of the eye are about equal. In comparison, the width is longer than the length in *G. guana*. In other words, the distance between the eyes on vertex is about the width of the eyes combined in *F. danforthi*. We have also observed variation in elytral color in specimens from Guana. One has the humeral flavous spot on the elytron extending narrowly to the midpoint, then widening to the apex. Some have the flavous, broad, humeral spot covering the whole elytron; in this case, the appearance is very similar to *G. guana*, but the antennae remain diagnostically bicolored, the eyes are not broader than long, and *F. danforthi* lacks the TSM.

7. *Mordellistena lineata* Ray

(Fig. 8)

Mordellistena lineata Ray, 1937.

Type Locality. Guanica, Puerto Rico.

Holotype. Male, 26.vi.1934, C. M. Matos; USNM 51601. We examined both the holotype and allotype.

Length: 1.6-2.2 mm. Form elongate, narrow, sides subparallel, attenuate, and rounded gradually caudad from apical third of elytra. Derm castaneous to black; frons of head, basal four segments of antenna, maxillary palpus, anterior and middle legs, and posterior leg other than femur flavocastaneous; a broad median stripe on each elytron flavocastaneous, reaching base of humerus, often narrowed in middle of elytral side margin, and extending to apex, leaving a narrow black line on each elytral side margin and a black sutural line. Surface covered with fine cinereous pubescence, except in the flavocastaneous area, where it partakes of the ground color.

Liljeblad (1945) has adequately redescribed the species except for the following characters: Metasternal plate with TSM. Middle tibia as long as its tarsus; penultimate segments of anterior and middle tarsi slightly enlarged and emarginate at apex. In addition to a short subapical ridge, posterior tibia with two long, oblique ridges, extending at least halfway across outer surface, basal ridge usually longer than the second, sometimes extending entirely across outer surface to genu. Posterior basitarsus with two, second with one, short oblique ridges; basal ridge on basitarsus sometimes rudimentary. Outer spur of posterior tibia 1/3 as long as inner one. Tarsal ratios: 3-2-3-4-6, 2-1-2-3-6, 3-3-4-6.

Pygidium long, almost three times as long as hypopygium, shorter in female, conical, attenuate to apex. Median protuberance of eighth sternite appearing bifurcate due to setae and a less sclerotized area all the way to base, ninth sternite twice as long as eighth with a less sclerotized area at apex; furca twice as long as tube or paramera, and as long as epimere; epimere twice as long as right parameron; ventral branch of right parameron narrowly branched out, basal prominence of left parameron set off its dorsal branch by a split. Penis three times as long as

epimere with apical first and third quarters enlarged, its apex terminating in a finger-like lobe with a lateral flange on each side as *Hipostenoda ambusta* (LeConte) (Lu et al. 1997).

Previous Records. Puerto Rico: Guanica (Ray 1937), Mona Island (Wolcott 1950). British Virgin Islands: Necker Island (Lazell 1995).

Material Examined. U. S. VIRGIN ISLANDS: Buck Island (9), St. Croix (3), St. John (29), St. Thomas (3) (MTSU). BRITISH VIRGIN ISLANDS: Anegada (2), Beef Island (4+3), Guana (74+85), Necker(4+6), Tortola (1+1), Great Camanoe (+5), Great Dog (+1), George Dog, 2, 30.ix.1996, *Lantana*, W. Lu (WL). PUERTO RICO: Mona Island, Casuarina plantation, 1, 7-13.xi.1992, malaise trap, Snelling and Torres (MTSU).

Remarks. The slightly enlarged and emarginate penultimate segments of anterior and middle tarsi are a giveaway character that this species does not belong to *Mordellistena*. The closest genus would be *Mordellina*, but the eyes are coarse and big in that genus, and the penultimate segments of anterior and middle tarsi should be the same as in *Mordellistena*. We retain this species in *Mordellistena* until we have a better understanding of the genera worldwide.

This species superficially resembles *Mordellistena angustiformis* Ray (1939), but the antenna is different from that species. In his original description, Ray stated, in an apparent lapse, that "seven apical segments of antennae" were flavocastaneous, lighter than basal segments. The reverse is true of all specimens we have examined, including the type. Ray also stated that the basal oblique ridge on the posterior tibia was "entirely across outer face." We find this character variable. Fewer than half the specimens examined are as described, all males. Most specimens have the basal ridge on the posterior tibia halfway across the outer surface or more, but not entirely, including both sexes. Occasionally the dermal color of some specimens is much lighter than black (probably newly emerged), but the even lighter stripes on elytra remain diagnostic. This is a very abundant species on flowers and dense vegetation, especially on leguminous *Acacia* species.

8. *Mordellistena irfianorum* sp. nov.

(Fig. 9)

Length: 2.2 mm. Form elongate, sides subparallel. Derm castaneous to black; mouthparts, maxillary palpus, basal four segments of antenna, anterior leg, tibiae and tarsi of middle and posterior legs testaceous. Surface covered with long whitish pubescence, slightly golden on scutellum and on elytra, but pubescence on side and sutural margins partaking dermal color from basal 1/5 on, leaving most side and sutural margins black, widened slightly in middle of side margin; underside pubescence longer.

Head small; eye hairy, and moderately granulated, reaching occiput, suboval, not emarginate behind antenna. Antenna filiform and long, reaching base of pronotum; segments 1 and 2 subequal, 3 and 4 shorter and narrower, 4 about 1/3 longer than 3; 5-10 each as long as 3 and 4 combined, increasing in width, 11 apically rounded, slightly longer than 10. Distal segment of maxillary palpus elongate-triangular, apical side slightly shorter than inner side.

Pronotum about 1/4 broader than long, sides rounded; basal angles acute, base arcuate, basal lobe conspicuous, rounded. Scutellum small, triangular. Elytra at most 2.5 times as long as broad, sides narrower at base than in middle, broadly rounded to apex; apices individually rounded. Metasternal plate with TSM.

Middle tibia as long as its tarsus; penultimate segments of anterior and middle tarsi emarginate (but not bilobed) at apex. In addition to a short subapical ridge, posterior tibia with two long oblique ridges, basal one extending entirely across outer surface; basal and second tarsal segments each with two short oblique ridges. Inner spur of posterior tibia 2/3 length of basitarsus, outer spur short, 1/4-1/5 length of inner one. Tarsal ratios: 1-1-1-2-3, 3-3-4-8-16, 3-4-5-9. Pygidium long, three times as long as hypopygium, conical, slender, and attenuate to apex.

Material Examined. U. S. VIRGIN ISLANDS: St. John, East Hope, Bordeaux Mountain., 900 ft., 1 female, 6-27.vii.1994, flight intercept trap, M. Becker and S. Bucklin (MTSU). PUERTO RICO: Cambalache, 1 female, 7.xi.1947, J. S. Caldwell (USNM).

Type Locality. 18°19'N, 64°43'W, St. John, U. S. Virgin Islands.

Holotype. Female, collected by M. Becker and S. Bucklin, 6-27.vii.1994, flight intercept trap, East Hope, Bordeaux Mountain, 900 ft., St. John, and deposited in MTSU.

Paratype. The remaining specimen from Puerto Rico.

Etymology. The Island Resources Foundation of St. Thomas, IRF, has provided support. We name this species for IRF in the genitive neuter pleural.

Remarks. This species looks very much like *M. lineata* at first glance and we have the same difficulty in placing it in any other known genus as we do for *M. lineata*. The two ridges on posterior second tarsus and the entirely black elytra distinguish it from *M. lineata*. The specimen from Puerto Rico is mutilated, missing antennae as well as tibiae and tarsi of most legs.

Acknowledgments

This article is dedicated to the memory of M. S. Collins, whose advice and encouragement were invaluable to this project and the career of WL. This project was funded in part by Island Resources Foundation, The Conservation Agency, The Edenwood Foundation, Rhode Island Agricultural Experiment Station, and Montana State University. We are indebted to P. W. Johnson, University of Rhode Island, for SEM work. Without a Smithsonian Institution Short Term Visitor Award to WL and the support of T. L. Erwin, this work would not have been completed.

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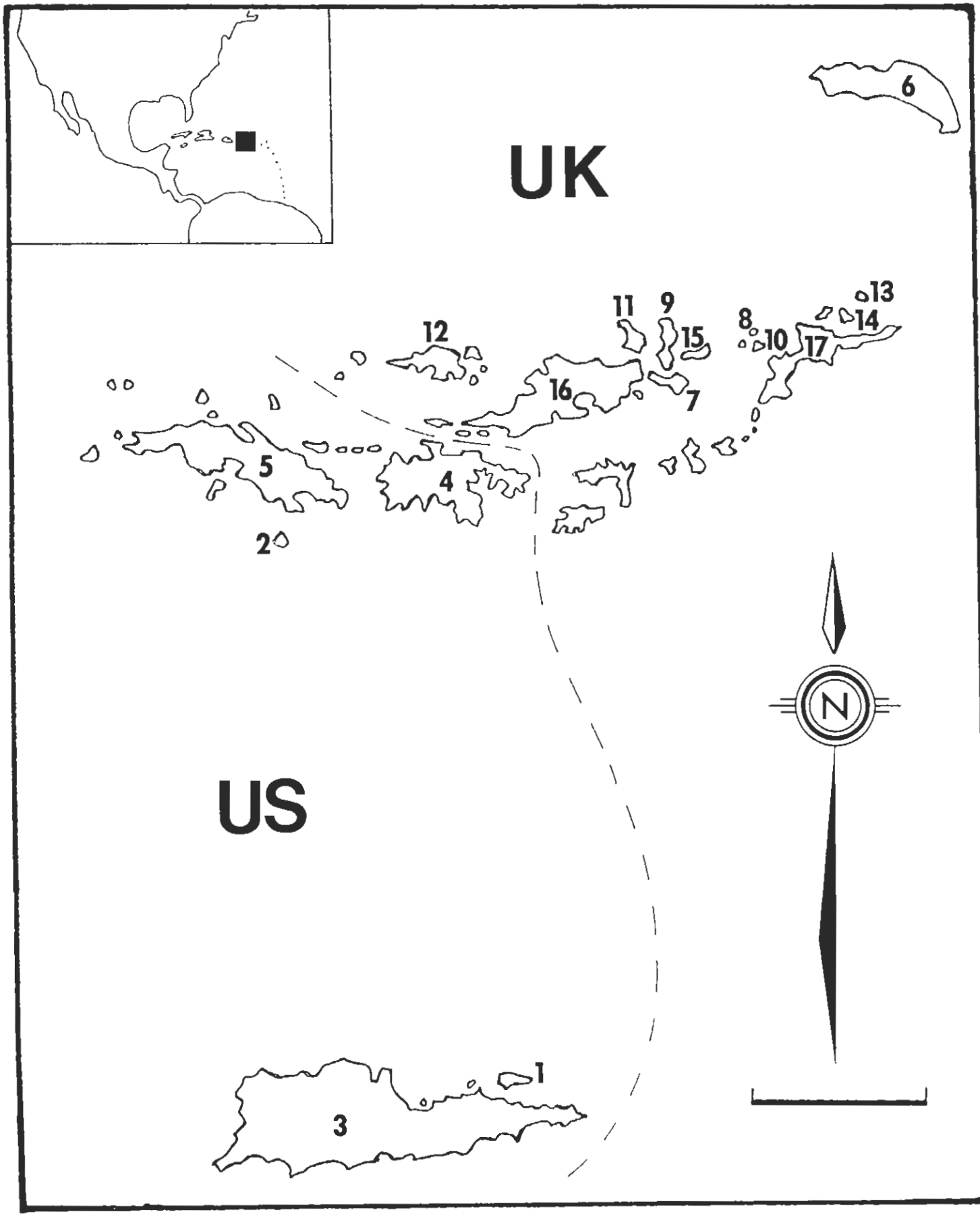
Received for publication _____; *accepted* _____.

Fig. 1. The Virgin Islands. US (American): 1, Buck. 2, Great St. James. 3, St. Croix. 4, St. John. 5, St. Thomas. UK (British): 6, Anegada. 7, Beef. 8, George Dog. 9, Great Camanoe. 10, Great Dog. 11, Guana. 12, Jost Van Dyke. 13, Necker. 14, Prickly Pear. 15, Scrub. 16, Tortola. 17, Virgin Gorda. Inset shows position, east of Puerto Rico and west of the Leeward Islands. Scale bar = 20 km.

Figs. 2-9. A, antenna; E, left elytron pattern; L, posterior leg; P, maxillary palpus; 8 and 9, male 8th and 9th sternites; LP, left parameron; RP, right parameron; D, dorsal branch; V, ventral branch; M, medial branch. 2, *M. atrata*. 3, *M. summermanae*. 4, *T. leucocephala* with sexual dimorphism in elytral patterns indicated. 5, *T. basifulva*. 6, *G. guana* with sexual dimorphism in antennae indicated. 7, *F. danforthi*. 8, *M. lineata* with ridge variation of posterior leg indicated. 9, *M. irfianorum*.

Fig. 10. SEM genitalic photos. b, basal prominence; d, dorsal branch; v, ventral branch; m, medial branch; otherwise as above. *M. summermanae*: A and B, LP with arrow showing a dent on medial branch; C, RP with arrow showing a prong on ventral branch. *T. leucocephala*: D, LP; E and F, inner and outer surfaces of RP with arrows showing a sharp basal angle of ventral branch. *G. guana*: G, lateral view of tip of penis with arrow showing a lateral flange; H, LP; I, RP. Scale bars A = 10 μm; B, C, and G = 30 μm; all others = 50 μm.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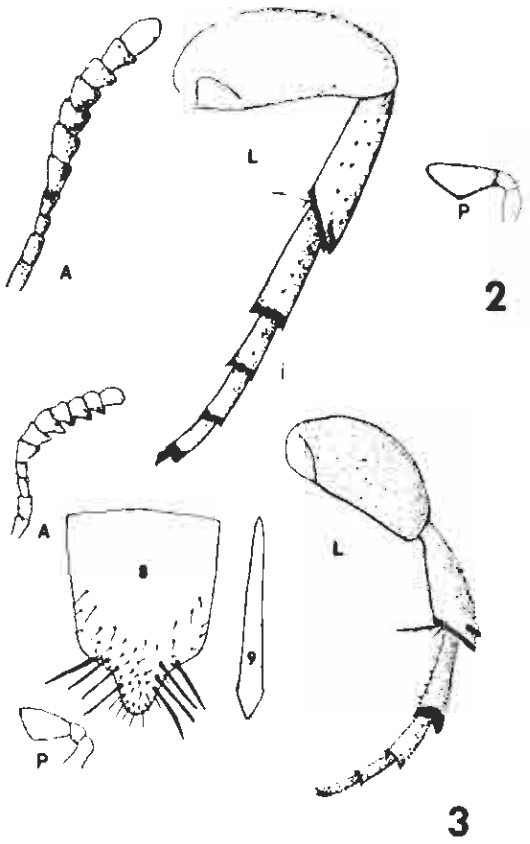
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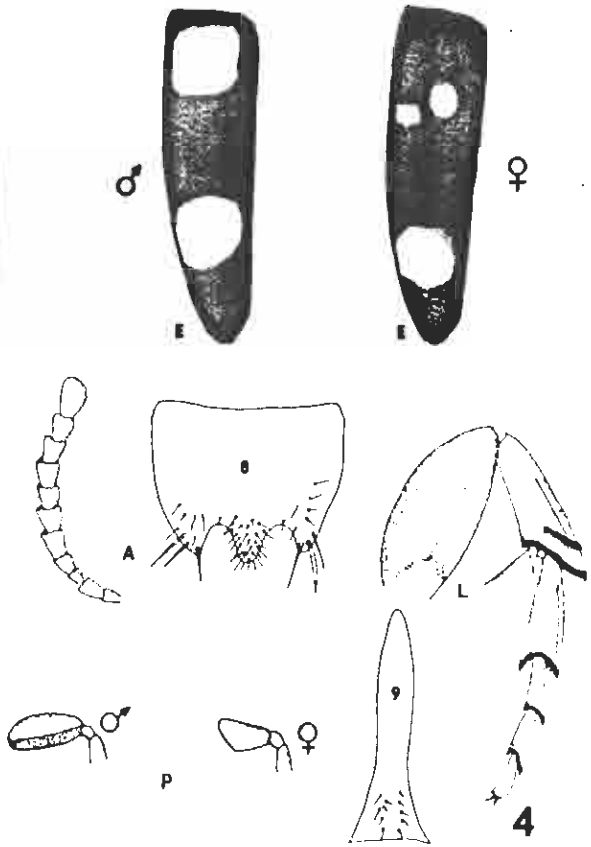
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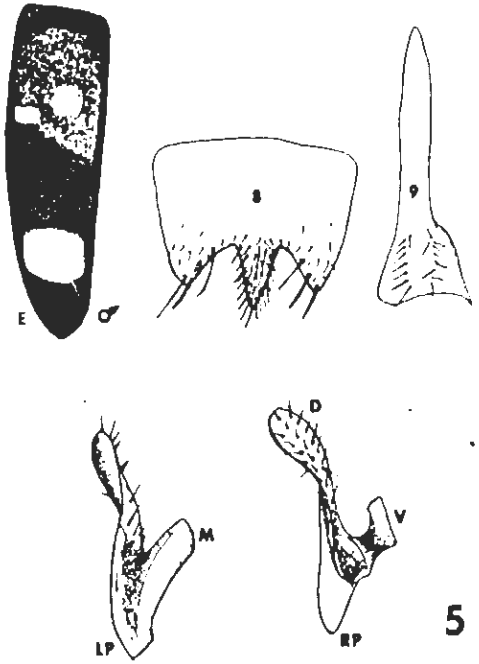
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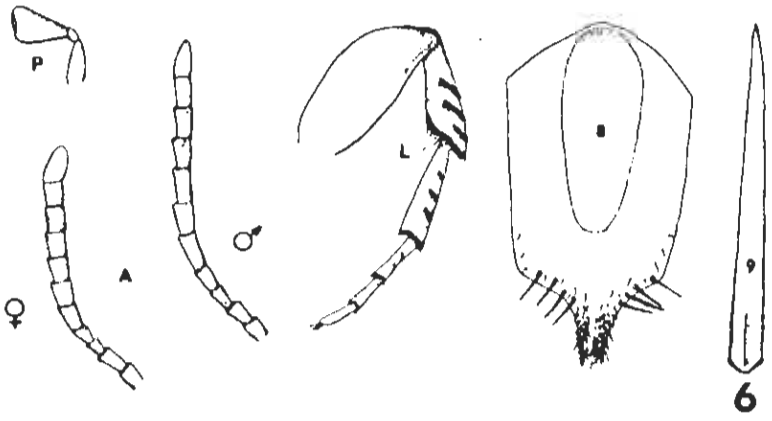

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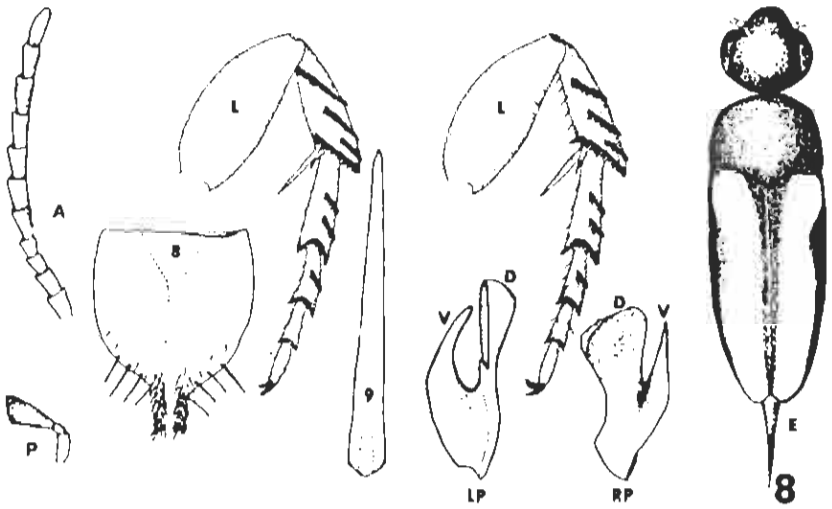

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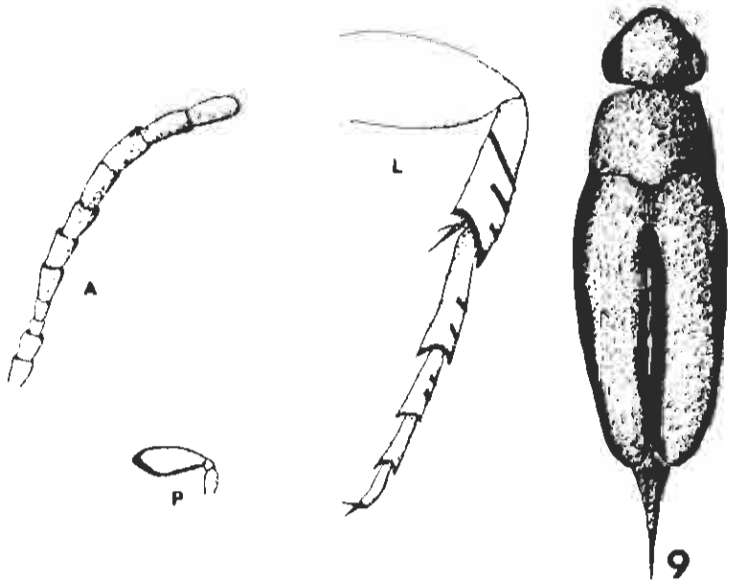

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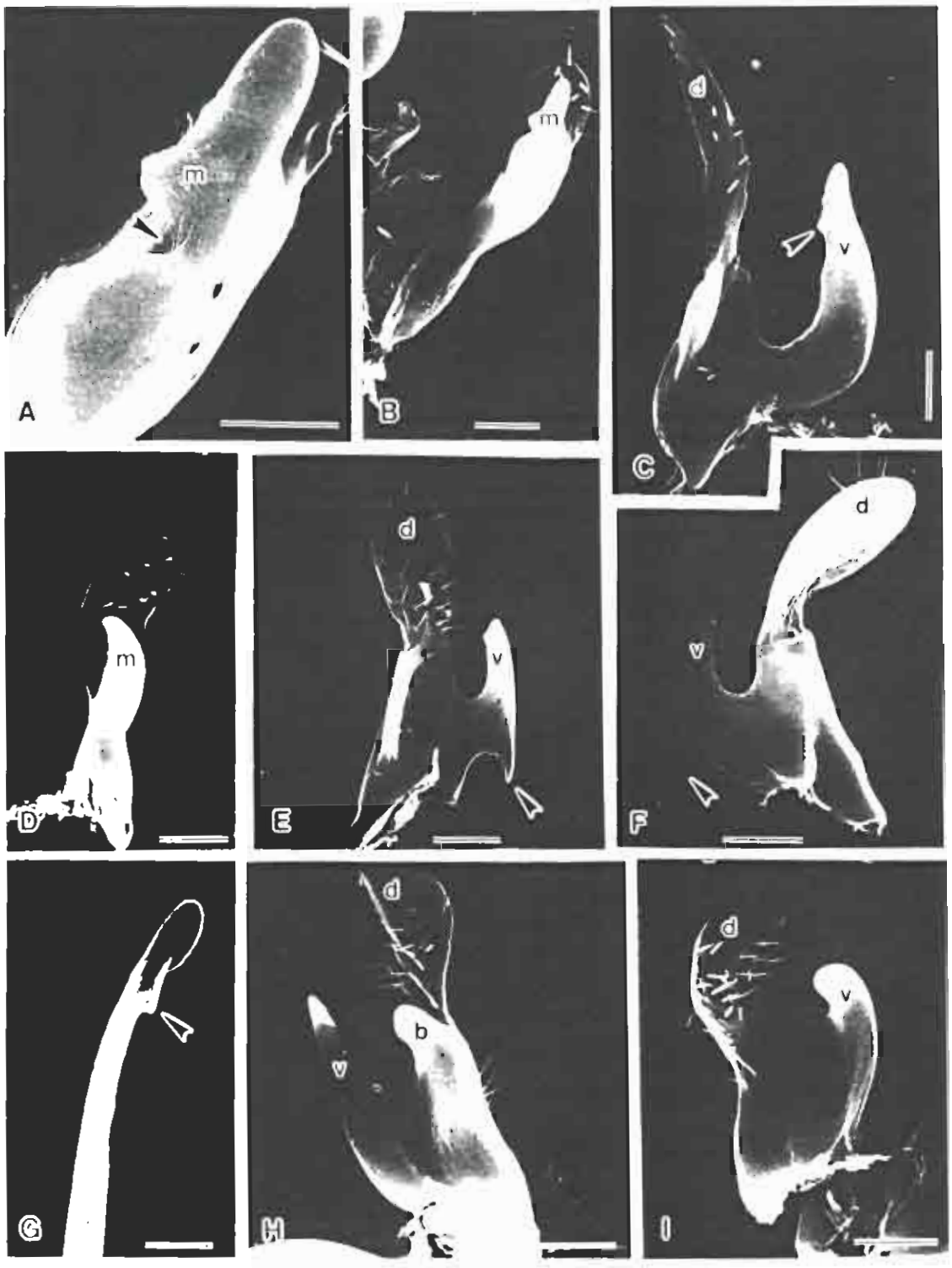
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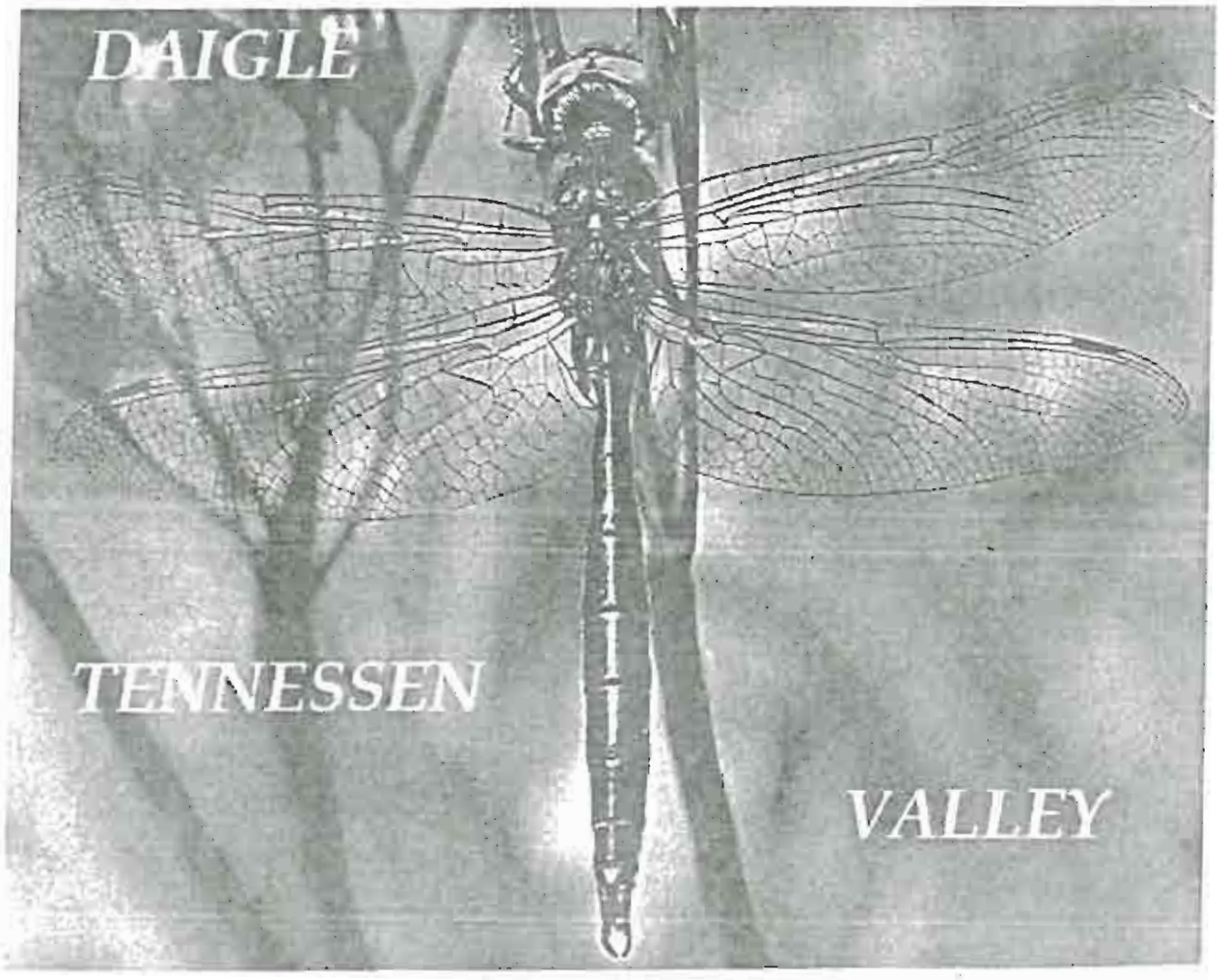

PUBLISHED BY THE DRAGONFLY SOCIETY OF THE AMERICAS

UNUSUAL INVASION OF DRAGONFLIES ON GUANA ISLAND, BRITISH VIRGIN ISLANDS

Fred Sibley

The dragonflies of the British Virgin Islands [BVI hereafter] have never been well studied - probably because there are very few species and very little habitat on this essentially arid group of islands. We found published records only for *Orthemis ferruginea* (Klots, E.B. 1932. Insects of Puerto Rico and the Virgin Islands. Vol. 14, part 1. NY Academy of Science.) and specimens for 3 others at the USNM [*Pantala flavescens* - Jose Van Dyke, *Ischnura ramburii* - Guana Island; *Erythrodiplax umbrata* - Tortola]. During October 1997 we recorded 10 species of odonates on Guana Island and Anegada Island although we could only find 3 species in 1998.

This paper reports on the unusual weather conditions in 1997 that brought so many species and so many hundreds of dragonflies to the BVI. Tentative speculations are made on the importance of such invasions in speciation.

Guana Island is a small arid island [about average precipitation for an BVI island] located about 2 miles north of the east end of Tortola [the major island of the group]. It is a little over a square mile in size with a maximum elevation of 850 ft. A small flat area on the sw side supports a brackish salt pond of several acres and two small freshwater seeps. These seeps do not have standing water during the dry season and in

some dry years may not have water for more than a few weeks. The brackish pond is always present and normally has a 1-3ft wide acres of bare ground between the water and the grass and scattered mangroves on edge. The pond was never used by dragonflies in 1997 or 1998. In 1997 dragonflies were frequently observed egg laying over the flooded lawn or in the flooded pond edge vegetation, but never on the pond side of the vegetation line. Flights over the pond were infrequent and even then individuals only ventured a few feet out from the vegetation before turning parallel to the shoreline. We were also on the island in Octobers of 1994-1996 but were not observing dragonflies. We returned in October 1998 and collected "normal year" data for comparison to the unusual events of 1997.

1997 OBSERVATIONS - During the period October 10 to 19, 1997 four of us were doing bird banding on Guana Island and casually tracking the dragonfly population. On October 10 there were an estimated 10-12 ***Orthemis ferruginea***, 12-15 *Erythrodiplax umbrata* and one *Ischnura ramburii* around or over the two seep areas - both seeps were already several times larger than in a normal year due to heavy rains before our arrival. These would appear to be the normal "residents" as the same three species were regular in October 1998. On October 12 the wind shifted to the SW as part of a major storm system bringing moisture out of the Pacific across Panama to the Caribbean. The wind continued out of the SW through the 15th with about 15 inches of rain occurring during the 4 day period. The salt pond doubled its size and overflowed onto the lawn. The seeps also increased dramatically in size and went from 3 inches deep to 3 feet deep. The maximum flooding occurred on the 14th with a continuous body of water from the dump seep at the SE end of the "flat" to the salt pond on the NE end. The two seeps receded fairly quickly to about twice their normal depth by the 18th. The salt pond only lost about 1/4 of the depth gained and continued to cover extensive areas of lawn.

Between the 10th and 14th there did not seem to be much change in numbers. The island list went from 3 to 5 with the addition of one *Erythemis vesiculosa* and a few *Tramea abdominalis*, but the total number of dragonflies did not change much. *Ischnura ramburii*, seen on the 10th, was not re-found until the 14th when a female was present.

On the 15th *Ischnura* became fairly common and easily found, and several *Tramea* and *Pantala* were seen over the lawn. Two individual *Perthemis domitia* were found the 16th and the numbers of *Tramea abdominalis*, *Tramea calverti*, and *Pantala hymenaea* shot up dramatically with further increases on the 17th (estimated several hundred individuals). Unfortunately there were no "dragonfly people" on the island and we failed to separate these three species adequately in the field. Based on collecting, *T. calverti* was the most common with 6 collected compared to 2 each for the other species. We collected a *Pantala flavescens* on Anegada Island and since we could easily separate it in the field from the *Tramea calverti* and *Pantala hymenaea* also present on Anegada felt that it must have been rare if not absent on Guana Island. A one-day visit was made to Anegada Island on the 19th. This is a flat coral island several miles wide and 15 miles long. We visited the major permanent fresh water pond on the island, The Slob. This is reported to be a hole dug down below the water table and normally about 10 feet across and a foot or so deep. When we were there it was several acres in size and knee deep within a few feet of the edge. *Orthemis*, *Tramea calvertii*, *Pantala hymenaea*, and *P. flavescens* were all present in that order of abundance [we did not differentiate *Tramea* and *P. hymenaea* at this time]. An *Anax junius*? flew over the pond briefly. There were water puddles everywhere but the only concentration of dragonflies was at The Slob although dragonflies were present in all the areas visited. No males were seen guarding the outlying puddles and most individuals seen away from The Slob were cruising at 3-8 feet and probably *Tramea* or *Pantala*. Anegada Island was not revisited in 1998 so we have no idea what a normal dragonfly population is.

DISCUSSION There is essentially no baseline data for the BVI so it is difficult to sort out the true importance of this invasion. ***Orthemis ferruginea***, ***Erythrodiplax umbrata***, and ***Ischnura ramburii*** were also present in 1998. A large healthy populations of all three were found on nearby Beef Island in a roadside ditch with permanent water. Only a few male ***Orthemis ferruginea*** were seen on Tortola. Since these three species were present on Guana Island before the SW winds arrived they are not considered as part of the unusual invasion. In a normal year we do not believe the fesh water seeps persist long enough to allow larvae to mature. Thus these species must be constantly recolonizing the island. If not on an annual basis then after every really dry year. *Erythemis vesiculosa* was not found in 1998 suggesting this species is a less regular

wanderer and recolonizer from the American Virgin islands or Puerto Rico. Although at least one individual was present before the 1997 storm later arrivals must also have been aided by the winds. All the rest of the species undoubtedly came from the west and arrived on Guana Island as a direct result of the unusual sw winds. ***Perithemis domitia*** is regular in the American Virgin Islands but no further east and ***Tramea calverti*** has not been recorded east of Puerto Rico. All the species could have come from Puerto Rico but, since they didn't start arriving in numbers until 3 days after the winds started must have come from further away or not started out until late in the storm. The continued increase in numbers after the winds shifted would suggest many individuals went past the island and then came back on the ne trades.

All species except ***Perithemis*** [only two males found] probably laid eggs on the island although, because of failure to separate some species, neither ***Tramea abdominalis*** or ***Pantala hymenaea*** were positively documented egg laying. We feel certain that none of the freshwater sources where egg laying was observed remained long enough for larvae to mature. In a normal year at least three species recolonize Guana Island. In the 1997 invasion of Guana Island, and presumably the whole BVI chain, 5 additional species attempted to colonize. All would have been successful if suitable habitat had been available. A 9th species attempted to colonize but only 2 males made it to the island. The *Anax* may be just a vagrant as one was seen in 1995.

We estimated, and probably severely underestimated, several hundred individuals of the 3 major invading species came to Guana Island. These were driven by the wind and presumably had little control over their destination so we must assume that other BVI islands with flooded fields were also visited by hundreds of individuals. Unless they were able to return to Puerto Rico or other islands to the west the reproductive potential of thousands of dragonflies was wasted on this attempt to colonize the BVI. This suggests there is always a huge surplus of individuals and that they are motivated to move by overcrowding. The dragonflies by their sheer numbers would guarantee a successful colonization with suitable habitat. The numbers would also insure the influencing of the resident gene pool on islands where the species was already present.

This just leaves lots of unanswered questions. Did this mass movement go far enough east to result in colonization of some of the Lesser Antilles by *Tramea calverti*? Are these mass movements from the west a common thing? Are mass movements from the east - much easier to imagine with the regular hurricanes and NE trades - also a regular phenomena? Is there reduced variation in Caribbean dragonfly populations because of the regular invasion or recolonization from a permanent source? If I hadn't been on Guana Island when this invasion occurred is there any way to infer its existence a year later?

Peck, 1992 [The dragonflies and damselflies of the Galapagos Islands, Ecuador. Psyche 99:309-321] reports on another group of arid islands and some interesting comparisons can be made to the BVI. The list of 8 species includes only one endemic. The author comments that the aridity of the islands and not the 1000 mile water gap is the reason for the limited fauna. This implies that invasions are easily possible. He also mentions that hawking dragonflies were exceptionally abundant along the coast after the unusual rainy conditions of the El Niño of January-May 1992. Suggesting what? An undetected invasion? A massive emergence? A swarming in response to storm conditions and a resultant invasion as the insects are carried by the wind? Certainly in the BVI there was no source for a massive emergence and the abundance with the El Niño rains had to be invasion. Despite the large number of scientist who have worked on the Galapagos Islands Peck is also plagued by lack of baseline data. He comments that ***Brachymnesia herbida*** had not been recorded since 1901 but was abundent during his visit in 1989.

I would like to speculate that all of the dragonflies on the Galapagos Islands [with the exception of an endemic ***Aeshna***] invade from the mainland in large numbers on a regular basis. Even once every 100 years would be enough to prevent speciation. Perhaps some of the species do not maintain a continuous presence on the island.

Barnett & Emms 1997 [Notulae Odonatologicae 4:153-155] reporting on the Chagos Archipelago. mention that ***Diplacodes trivialis*** is regularly found on islands in the groups which have no water. This would be similar to the situation I propose for the three "resident" species on Guana Island. The large number of individuals present may not include any individuals raised on the island and they may not produce any descendants. The 3 most common species on Guana Island in 1997 were not even present in 1998 and it is likely the total number of individuals emerging on the island in most years is

zero. Since I'm primarily a bird person and have now spent 5 Octobers observing and banding birds on Guana Island I'm fascinated by the apparent ease by which dragonflies recolonize the island compared to birds. In the last decade two species have become extirpated on the island after hurricanes decimated their populations. Both the Smooth-billed Ani (Crotophaga ani) and Northern Mockingbird (Mimus polyglottus) are common on parts of Tortola and Beef Island only a mile away and the birds could reduce the water crossing to as little as 200 yards. The habitat on Guana Island is suitable, the distances are no challenge but neither species has returned to Guana Island. The Bananaquit (Coereba flaveola) is abundant in the Caribbean and each island group has a recognizable subspecies. This is not unusual for the birds of the Caribbean where many species have splintered into numerous forms. On Guana Island we have banded several hundred individuals and they exhibit a reluctance to disperse even a half mile through suitable habitat. The birds do not seem to disperse as far in their lifetime as a non-territorial dragonfly travels in one day. Is there a real difference between island speciation in birds and dragonflies or are we dealing with just a limited number of dragonfly species that easily and regularly invade distant islands?

ACKNOWLEDGEMENTS Special thanks to Henry and Gloria Jarecki who make their nature sanctuary island available to researchers, to the Falconwood Foundation for supporting the study and to Dr. James Lazell, The Conservation Agency, for innumerable instances of assistance, support and encouragement. Thanks also to Peggy Sibley, Judy Richardson, Alison Oliveri, and Eric Lazo-Wassem for assistance
with field work.

1997 - SPECIES LIST AND COMMENTS

Ischnura ramburii - Single male on 10th, female on the 14th and common 15th to 18th, but no more than 8 seen in any one day. 4 males 2 females collected.

Anax sp? probably ***junius*** - One seen briefly on Anagada Island.

Erythemis vesiculosa - Seen on 5 days and never more than 2 individuals, but must have been present from 11th on. Single female egg laying on 14th in mat of floating vegetation and another egg laying on 18th in flooded grass at edge of lawn accompanied by male. 1 male, 1 female collected.

Erythrodiplax umbrata - Present every day. Less common than ***Orthemis*** but numbers constant throughout stay. No mating or egg laying observed but 4 females caught [2 with dark wings]. 5 males, 4 females collected

Orthemis ferruginea - The commonest of the "resident" species. About 10 estimated at dump first day. This is consistent with 1988 observations where 8-10 seemed to be the maximum number of territories available [but 35 males caught]. Definite females of this species were observed egg laying accompanied by males on the 11th and 12th. Commonest of 4 species at The Slob on Anegada. 7 males collected on Guana and 6 on Anegada.

Pantala flavescens - Rarest of the four species on Anegada and not seen on Guana Island. One male collected.

Perithemis domitia - Two males found floating in oily scum on dump pond the 16th. These appeared to be dead but several hours later they had revived enough to flap wings. The three species below were not separated in the field. It is thus difficult to know if the essentially random collecting, but all near water, reflected the true proportions. These three made up the bulk of the hundreds of individuals present and showed up well away from the water. Seen frequently from 16th on at the hotel [300 ft level] and over the unflooded lawns hawking at levels of 5-20 feet.

Pantala hymenaea - 2 males caught on Guana, 1 on Anegada Collected on 17th over flooded lawn and as one of 3-5 feeding over large brushy area.

Tramea abdominalis - 2 males caught on Guana Collected on 13th over flooded garden area and on 17th over flooded lawn.

Tramea calverti - 4 males and pair caught on Guana, 2 males on Anegada. Pair and male collected over flooded lawn on 17th and three males collected in same area on 18th.

Subj: **Re: BVI dragonflies**
Date: 01/22/1999 8:12:19 AM Eastern Standard Time
From: smiller@icipe.org (Scott Miller)
To: fred.sibley@yale.edu (Fred Sibley)
CC: smiller@icipe.org, jcinjtown@aol.com

I vaguely recall that dragonflies might have been abundant in Buntin Ghut, but don't have any way of verifying that here. Skip was with me when I was there, and this is the kind of thing that he might have noted in his field notes. By copy of this, I'm asking Skip if he has notes about dragonflies in Buntin Ghut in July 1984 (wow! 15 years ago!).

>> From: Fred Sibley[SMTP:FRED.SIBLEY@YALE.EDU]
>> Sent: Thursday, January 21, 1999 8:34:10 PM
>> To: Scott Miller
>> Subject: Re: BVI dragonflies
>> Auto forwarded by a Rule
>>
>Thanks for the quick reply.
>
> In July 85 you had Ischnura ramburii from both Guana Island and Zion Hill
>on Tortola - Skip not here now so can't ask him where that is.
> July 84 you had 3 Erythrodiplax umbrata on Tortola at Buntin Ghut and an
>Orthemis ferruginea on Guana Island.
>
> Hope this jogs some memories - would be very interested in any place on
>Tortola that has dragonflies - did a day of wandering around over there
>without finding anything but a few temporary pools with one Orthemis each.
>
> Thanks for the contact at Bishop Museum.
>
>
>At 11:05 PM 1/21/99 +0300, you wrote:
>>Thanks for the note. I was on Guana (with short visits to other BVI) in
>>July of
>>1984, 1985, 1986, 1987, 1988, October 1989 and October-November 1990.
>>Collections from 1984-1986 are deposited at USNM, those of 1987-1990 at
>Bishop
>>Museum. I did not put much effort into dragonflies, but would have picked
>them
>>up when possible, by hand and Malaise trap. I have a vague recollection of
>>them being very abundant in one canyon on Tortola in one year (although I
>>probably only visited this canyon one year) -- if you send me the label data
>>maybe that will jog my memory. I would not have kept any specific notes on
>>them.
>>
>>You could try contacting Gordon Nishida (gordo@bishopmuseum.org) regarding
>the
>>specimens at Bishop.
>>
>>
>
>Fred Sibley
>Collection Manager (Retired) - VZ
>Peabody Museum, Yale Univ., P.O. Box 208118, New Haven, CT 06520-8118
>home address and phone 25 Shirley St., Naugatuck, Ct 06770

United States Department of Agriculture | Forest Service | Forest Products Laboratory | PO Box 1377 Luquillo, PR 00773 USA

Dr. James Lazell
The Conservation Agency
6 Swainburne Street
Jamestown, RI 02835

Phone: 787-889-7445
FAX: 787-888-5685

Dear Skip:

July 1998

I thought I'd drop you a line to let you know we are making some headway on publishing the ectomycorrhizal fungal symbionts on Guana Island. As I've long suspected, the gray *Amanita* that comes up in the sand near *Coccoloba uvifera* is and undescribed species. We're still in the process of choosing a name for it - not easy in a genus with hundreds of named species already. Enclosed is a draft manuscript with some attached revision pages, including an acknowledgement the Conservation Agency. I never did hear if Gloria Jarecki received the big package of photos I sent.

I was wondering if there was an opportunity to go back to Guana this October to try for more ectomycorrhizal fungi. I'll be in England most of October, from the 9th to the 27th, so I don't have much of a window for a Guana Island trip, but I would still like to come for a few days. I leave for a vacation (bird-watching) in S. Africa on August 6 and don't return until the 31st.

With best wishes,

D. Jean Lodge, Botanist
Center for Forest Mycology Research

New Title: New and Interesting Ectomycorrhizal Fungi from Puerto Rico and Guana Islands, Greater Antilles

Add Island or Isl. after Guana throughout the text.

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 elev., but the collections reported on here were from 1--500 m elev. 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 & 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 mean a 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 the 59 species surveyed were associated with arbuscular mycorrhizal fungi, but about 5% of are also associated with basidiomycete fungi (Lodge, 1996). The presence of agarics which are known to be ectomycorrhizal associates of tree hosts in these forests leaves little doubt about the presence of ectomycorrhizal symbioses. Lodge (1987, 1996) reported the presence of thick mantles of basidiomycetous hyphae with clamp connections on the roots of *Pisonia subcordata* Sw. (Nyctaginaceae), *Coccoloba swatzii* Meisn., and *C. pyrifolia* Desf. (Polygonaceae), and ectendomycorrhizae in *Andira inermis* (W. Wright) DC (Papilionaceae). In Cuba, Kreisel (1971) demonstrated the presence of ectomycorrhizae in the sea grape, *Coccoloba uvifera* (L.) L. The

fungi reported in this paper are most likely associated with these hosts and potentially also with *Hymenea courbaril* L. (Caesalpiniaceae) in subtropical moist forest and *Chrysobalanus icaco* L. (Rosaceae) in coastal sand dune communities. Although there are undoubtedly other ectomycorrhizal hosts in these forests, some of the putative hosts reported by Pegler (1983) for the Lesser Antilles are dubious and need to be confirmed.

Instead of the name *A. albivolvata*, I suggest something that means sand-loving, such as *A. arenicola* or *A. psammophila,* but perhaps these have already been used for other species. The first is preferable because sand is arena in Spanish. Another possibility is *A. playera* because a beach-goer is a a playera in Spanish. Note that our field station is Sabana, not Savana, so don't use a species eipitat of savana. Besides, savana means an open grassy area with scattered trees, which does not characterize the chicken farm site. The site isn't even in bario Sabana, even though it is above the Rio Sabana. If it is indeed a new species, perhaps *P. luquiensis* would work better, for Luquillo, the name of the Munucipio and the nearest town. It is actully closer to Luquillo than Sabana.

Acknowledgements:

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New and Interesting Higher Fungi from Puerto Rico and Guana Islands

Orson K. Miller Jr.
Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061

Timothy J. Baroni
Department of Biological Sciences, SUNY-College at Cortland, Cortland, NY 13054

D. Jean Lodge
Center for Forest Mycology Research, United States Department of Agriculture, Forest Service, Forest Products Lab., PO Box B, Palmer, Puerto Rico 00721

Abstract: Reports of ectomycorrhizal fungi from Puerto Rico and Guana in the Greater Antillies include two new species of *Amanita*, one *Lactarius* and a new *Phlebopus*. In addition, new distribution records of *Russula littoralis* Pegler and a possible new small spored *Phylloporus* are reported. Ectomycorrhizal hosts include *Coccoloba uvifera* (Polygonaceae) and putative hosts *Hymenia courbaril* (Caesalpiniaceae) and *Andira inermis* (Papilionaceae)

Key Words: Basidiomycetes, systematics, *Amanita*, *Lactarius*, *Russula*, *Phlebopus*, *Phylloporus*, Greater Antillies, Puerto Rico, Guana

INTRODUCTION

Puerto Rico and Guana are both islands which lie within the Greater Antilles and have tropical climates. The areas surveyed range from sea level to 500m elevation. Coastal dune communities are present in these habitats along with subtropical wet forest according to the Holdridge system (Ewel & Whimore, 1973). The Luquillo Mountains of NE Puerto Rico was most intensively sampled and this area has a mean annual rainfall of 392cm/yr and a mean monthly temperature of 24-27°C. Much of the sampled area lies within the tabonuco forest zone which is reported to have in excess of 152 tree species (Lodge, 1988). The majority of the tree species are associated with vesicular arbuscular (VA) mycorrhizae (Lodge, 1996). However, the presence of agarics which are known to be ectomycorrhizal associates of tree hosts in the tropical forest leaves little doubt that there are a few ectomycorrhizal tree species. In fact Lodge (1996) reports the pesence of "thick mantles of basidiomycetous hyphae with clamp connections"on the roots of *Pisonia subdordata, Coccoloba swartzii, and C. pyrifolia.* The fungi reported in this paper are

most likely associated with several putative ectomycorrhizal hosts including *Coccoloba uvifera,* in the Polygonaceae, *Hymenaea courbaril L.* in the Caesalpiniaceae and *Andira inermis* (W.Wright) H.B.K. in the Papilionaceae. However, there are several other tree species present in one area where two ectomycorrhizal taxa were found but they all appear be associated with VA mycorrhizae. The number of ectomycorrhizal hosts in tropical forests is not large and as yet not totally known. There are some well known genera such as *Coccoloba* which are notable exceptions.

Color comparisons were made using Methuen (1967) and designated Met 6 E-4 which indicates the page, row and color block. In some cases the pileus coloration was recorded using Cailleux (1948) and indicated as Caill.T73 which indicated row T and block 73. Chemical reagents including Melzer's solution, Gum-guaiac, 2% Phenol and Ferric sulphate were used when appropriate and the reactions recorded along with smell and taste.

Amanita "cystidiosus" O.K. Miller et D.J. Lodge *sp. nov.* FIGS. 1-4,19.

Pileus 2.0-4.7 cm broad, convex to plane in age, subviscid when wet, fine mealy remains of univesal veil on the surface, pale straw yellow, margin finely sulcate-striate. *Lamellae* free, subdistant, ventricose, 2 tiers of lamellulae, light yellow to yellow in age. *Stipe* 1.9-5.2 cm long, 0.4-0.7 cm wide, equal with an abrupt round basal bulb, dry, white except bulb which has yellowish remains of the universal veil. *Partial veil* remains as a persistent, cothurnate, annulus. *Context* firm, white. Smell not distinctive. *Pileipellis* of interwoven, broad, thin-walled hyphae 4.2-20 µm diam. *Partial* veil of filamentous, thin-walled, hyphae 5-9 µm diam. Universal veil of interwoven thin-walled, hyphae 4.0-13.0 µm diam with distinctive clavate cells 15-27 µm diam. *Clamps* absent. *Cheilocystidia* 45-55 x 7-11 µm clavate to subfusiform, thin-walled, protruding one-half to one-third. Basidia 25-30 x 8-9.5 µm clavate, thin-walled, 4-sp'd. *Basidiospores* 7-9 (-10.5) x (4.8-) 5.5-6.0 µm (E_m = 1.34: E 1.15-1.53) short elliptic, thin to slightly thick-walled, non amyloid in Melzer's solution. In sand dunes under *Coccoloba uvifera,* Piñoines Commonwealth Forest, near Loiza, PR, Jan. 14, 1998. typus legit: O.K. & H. Miller, D.J. Lodge OKM 27232 (VPI).

Pileus 2.0-4.7 cm broad, convex to 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 of the bulb which is covered with the appressed remains of the universal veil and is yellowish (near Met 4A2), fine white rhizomorphs emenate 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, stip white 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 x 7-11 µm clavate, narrowly clavate to subfusiform, thin-walled, protruding one-third to one-half, numerous. *Basidia* 25-30 x 8-9.5 µm clavate, thin-walled, 4-sp'd hyaline in 3%KOH and Melzer's solution. *Basidiospores* 7-9(-10.5) x (4.8-)5.5-6 µm (E_m = 1.34:E 1.15-1.53), short elliptic, thin to slightly thick-walled, non-amyloid in Melzer's solution. *Spore print* pure white.

Habit, habitat, and distribution: in sand in the dunes or fore dunes among or close to *Coccoloba* and a wide spread vine; Piñones Commonwealth Forest, Beach near Loiza Jan. 14, 1998.

Material examined: **USA**: **Puerto Rico**, Piñones Commonwealth Forest, beach near Loiza, Jan. 14, 1998 Coll. D.J. Lodge, O.K. & H. Miller OKM 27232, OKM 24234 (VPI).

Observations: A taxon meeting this description has not been collected before on Puerto Rico. The species is in the subgenus *Amanita*, section *Amanita*. Note that OKM 27234 and OKM 27232 are the same taxon and were collected as we moved down the beach all associated with *Coccoloba*.. The persistent, membraneous white annulus which flares out; 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 characters which are very distinctive. The spores are non-amyloid, short elliptic with a thickened wall. Fresh characteristics are from OKM 27232. The presence of cystidia is a first report. Jenkins (1977) study of the North American taxa in the section 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. "*cystidiosis*" are derived from the lamellar trama and not remnants of a tissue differentiated during primordial development. Recently described species of *Amanita* by Tulloss (1989, 1990, 1995) and Tulloss et al. (1992) do not contain a taxon related to A. *cystidiosus*.

arenicola? psammophila? playera? guana?

Amanita "*albivolvata*" O.K.Miller & D.J. Lodge *sp.nov.* FIGS. 5-8

Pileus 3.5-5.5 cm broad, depressed to infundibuliform, moist, smooth, drab gray with pale buff universal veil patches in the center, margin with plicate striations. Lamellae free, narrow, close white, one tier of lamellulae. 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. *Universal veil* of filamentous, hyaline hyphae intermixed with a nearly equal proportion of globose, subglobose, to pear shaped hyaline, thin-walled cells. *Basidia* 35-55 x 12-14 µm clavate, thin-walled, 4 sp'd, hyaline. *Basidiospores* 9-12.5 x 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, non-amyloid in Melzer's solution. In sandy soil under *Coccoloba uvifera* on Piñones beach near Loiza, Mun. Rio Grande, Puerto Rico. Typus legit J.Trappe, M. Castellana & J. Lodge, PR-4717

Pileus 3.5-5.5 cm broad, strongly depressed to infundibuliform, moist to sticky, sand covered, smooth, Drab Gray, with flat pale buff (124) ditersile patches of universal veil in the center, margin evenly pale Drab Gray 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 with the ragged remains of the veil in the sand or adhearing 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. No clamps seen on any tissue. *Universal veil* of filamentous, hyaline hyphae intermixed with a nearly equal proportion of globose, subglobose, to pear shaped hyaline, thin-walled cells *Cheilocystidia* infrequent to frequent, of pyriform to subglobose or globose cells 18-30 x 13-17 µm thin-walled, hyaline. *Basidia* 35-55 x 12-14 µm clavate, thin-walled, 4 sp'd, hyaline. *Basidiospores* 9-12.5 x 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, non-amyloid in Melzer's solution..

Habit, habitat, and distribution: in sandy soil under *Coccoloba uvifera* on Pinones beach near Loiza, Mun. Rio Grande, fruiting in December.

Material examined: **USA**: **Puerto Rico**; Mun. Rio Grande, Pin-ones beach near Loiza, 12/23/1997, coll. J.Trappe, M. Castellano & J. Lodge PR-4717. **Guana Island**: White Beach Rd., 10 Oct. 1997, coll. D. Jean Lodge, GUA 109.

Observations: The non-amyloid spores, 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 white, saccate volva; buff volval patches at the cap center and the distinctive type of universal veil tissue are characteristics of the species. The habitat in beach sand, often in fore dunes under *Coccoloba* is a distinctive habitat. The pileus coloration and anatomic details of the universal veil combined with differences in spore size are quite different from the two taxa in Section *Vaginatae* with a membranous universal veil described by Tulloss et al. (1992). No taxon described by Coker (1917) or Jenkins (1986) has the combination of characteristics described above for A. *cystidiosus*.

Lactarius "*coccoloba*" O.K. Miller & D.J. Lodge *sp. nov.* FIGS. 9-14, 20.

Pileus (1.8-) 5-11 cm broad, robust, plane in age, dry, dull cream but soon stained mottled brown to black-brown. *Lamellae* adnate, crowded, white at first, brown in age, latex white stainscut or bruised surface dark brown. *Stipe* 2-4 cm long, 1.2-2.2 cm wide, dry, smooth at apex, minutely hairy below, dull white stained brown to dark brown. *Context* firm to tough, white at first, stains dull brown when cut or bruised. *Pileipellis* a turf of pileocystidia 24-65(-122) x 3.6-5.4 µm

cylindric to fusiform. *Subpellis* of interwoven, gleatinized hyphae 2.7-4.5 µm diam. *Basidia* 60-79 x 8.1-9.5 µm clavate, thin-walled, 2 to 4sp'd. *Basidiospores* 7.2-9(-10) x 5.8-8.4 µm, (E_m = 1.26: E 1.13-1.55) subglobose with a subapical plage and low (<0.3 µm high)amyloid warts and weak partial amyloid reticulations. In sand dunes under *Coccoloba uvifera*, Pinones Commonwealth Forest, Loiza, PR, Jan. 14, 1998.Typus legit: D. J..Lodge, O.K.& H. Miller OKM 27240 (VPI).

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 smooth in buttons straightens out in age. *Lamellae* adnate, crowded, white at first, with a white whey-like latex which stains the gill where cut dark brown, 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, just at base a dark black-brown area. *Taste* sweet and mild. *Smell* strongly of fish or herring like *L. volemus* and is a room filling odor persisting in dried material.

Pileipellis an irregular turf of pileocystidia 24-65 (-122) x 3.6-5.4 µm cylindric or tapering toward apex, thin-walled, hyaline or with light brown slightly thick-walled, arise 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, interwoven hyphae 4.5-10.5 µm diam, a textura intracata, filamentous, rectangular to irregular thin-walled, 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 latiferous hyphae. *Caulocystidia* 39-45 x 3.6-5.4 µm cylindric to narrowly fusiform, occasionally subcapitate, thin-walled, hyaline or with a light brownish hue in 3%KOH, numerous.. *Cheilocystidia* 35-65 x 2.5-5 µm hyphal-like, fusiform with an apical projection to narrowly clavate, thin-walled, hyaline, protruding only slightly if at all, scattered not frequent. *Basidia* 60-79(-85) x 8.1-9.5 µm clavate, thin-walled, 2 to mostly 4sp'd, sterigmata 5.5-7 µm long. *Basidiospores* 7.2- 9 (-10.8) x 5.8-8.4 µm, (E_m = 1.26: E = 1.13-1.55) subglobose with a subapical plage, and short hyaline apiculus, fine very low (< 0.3µm) amyloid warts and weak partial reticulations.

Habit, habitat, and distribution: in sand on dunes under Coccoloba uvifera L., Piñones Commonwealth Forest, Beach near Loiza, PR, Jan. 14, 1998.

Material examined: **USA** : **Puerto Rico**; Piñones Commonwealth Forest, Beach near Loiza. Jan. 14, 1998. Coll. J. Lodge, O.K. & H. Miller OKM 27240 (VPI)

Observations: This is a distinctive taxon not collected before in Puerto Rico and not recorded in other Caribbean works on the Agaricales. It is a very robust species, with adnate, close to crowded lamellae and a short stipe and sporophores which are very close to or buried in the sand. It stains 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, herring-like odor persists in the dried specimens, which are very tough. Material soaked in 95%ETOH 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 hyphal-like to narrowly clavate. It also has numberous caulocystidia. It is a member of the Subgenus *Lactifluus* and the section *Lactifluus* (Hessler and Smith, 1979). It does appear to be closely related to *L. caribaeus* Pegler (Pegler 1983) with similar microscopic anatomy, especially the low individual warts which form the spore ornamentation, and the spore size, although the basidia are distinctly shorter. However, there are distinctive macroscopic differences. The lamellae of *L. caribaeus* are deeply decurrent, subdistant with "numerous lamellulae of two lengths" and illustrated by Pegler (1983, Fig. 123A .and color Plate 20C). The stipe surface is described as pure white at first and glabrous. It is found associated with *Coccoloba pubescens* and *C. diversifolia* in "degraded xerophytic forests" and not in a similar dune habitat. Both of these taxa are distinctly different from any taxon now placed in the section but they have several characters common with *L. luteolus Peck.* Firstly the cystidia are thin-walled in our material and the taste is mild. *Lactarius. luteolus* Peck is not a robust spcies and has a different but similar pileipellis, smaller basidia, higher ornamentation on the spores and is not a robust taxon. 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. cocoloba* are soaked in 95% ETOH. It seems that the two taxa from the Lesser and Greater Antillies have evolved over an extended period of time with species of *Cocoloba* on islands separated from each other. They are closely related but sufficient genetic drift has occurred to easily distinguish them by their macroscopic characteristics.

Phlebopus ("savana") O.K. Miller & T.J. Baroni *sp. nov.* FIGS. 15-18, 21.

Pileus 2.6-7.1 cm broad, convex, felt-like, dry, smooth, black-brown to deep red-brown, margin incurved until mature. *Pores* adnate, pustulate at first, 2-4 mm deep, 3-4 per mm, uneven at maturity, yellow, gradually staining light blue when bruised. *Stipe* 2.5-5.0 cm long, 0.9-2.1 cm wide at apex , forming a clavate base 1.7-2.8 cm wide, yellowish or black brown just at apex black-brown overall with a fine network of yellow mycelium over the surface, light brown rhizomorphs at the base. *Pileipellis* a narrow layer of hyaline, gelatinized hyphae 2.5-6 µm diam. *Tube trama* of divergent, thin-walled hyphae 3.4-5.5 µm diam. *Cheilocystidia* abundant 28-55 x 6-12 µm , clavate to broadly clavate, thin-walled. Basidia 30 x 9 µm diam, clavate, 4-sp'd. *Basidiospores* 5-6.8 x 3.8-5.5 µm diam (E_m = 1.29: E 1.09-1.52) elliptic, thin to slightly thick-walled, olivaceous-brown. *Spore print* olive-brown. On the ground under hardwoods, near Savana Field Station above the Chicken Farm, PR. Jan.. 15, 1998. Typus legit: D.J. Lodge, O.K. & H. Miller. OKM 27252(VPI).

Pileus 26-71 mm broad, broadly convex, felt-like, dry, smooth, black-brown to deep red-brown [Caill.T73; Met 7F4-6,9F3-4], margin incurved until maturity. *Pores* adnate, 2-4 mm deep, 3-4 per mm, pustulate at first, opening in age, uneven at maturity, yellow (Met 4A 4-6) gradually

staining light blue when bruised. *Stipe* 2.5-5.0 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 network of yellow 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 which persists in the dried collections. *Taste* mild.

Pileipellis a narrow layer (40-65 µm thick) of hyaline gleatinized 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 x 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 KOH and Melzer's solution

Basidiospores 5.0-6.8 x 3.8-5.5 µm (E_m = 1.29: E = 1.09-1.52) elliptic, thin-walled to slightly thick-walled, olivaceous-brown. Spore print olive-brown (Met 3E4-5).

Material examined: **USA**: **Puerto Rico**; near Sayana Field Station, June 10, 1998, Coll. D.Jean Lodge, O.K. & H. Miller OKM 27200. June 15, 1998 Coll. H.& O.K. Miller, OKM 27252, OKM 27254.

Habit, habitat and distribution: on the ground on a roadway under hardwoods, on a well drained site, at 300' elev. near Savana Field Station above the Chicken Farm, (ST-MW FOREST), fruiting in June.

Observations: 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 fine yellow, sparse mycelium [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 and all specimens are evenly or nearly evenly colored with a conspicuously incurved margin. Note that in the same collecting location two additional bolete collections (OKM 27252 & OKM 27254) were found on Jan 15th. Collection OKM 27252 was 9.5 cm broad, the cap color had faded to red-brown in the center (Met 6F 5-6) the rest orange-brown (Met 5C 5-6) but the rest of the fresh characteristics were of the same as the specimens described above. The additional collection, OKM 27254, was some distance from the two mentioned above but was old and mature but has the same spores and other microscopic characters as the other two collections.

Phylloporus sp.

Pileus 22 mm broad, moist, somewhat felt-like, orange-brown. *Lamellae* lamellate near the stipe to poroid over the margin, 2-3 mm thick, very irregular, yellow orange, no blue staining observed when bruised. *Stipe* 14 x 4 mm equal, moist, smooth, yellowish. *Context* light buff, firm, bruising pinkish.

Pileipellis a trichoderm composed of narrow, nearly cylindric to narrowly fusiform thin-walled, hyaline cells 34-93 x 3.5-5.0 µm diam arise 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 hyphae, on average somewhat larger than the pileipellis cells, hyaline. *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 x 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 x 8-9 µm narrowly clavate, thin-walled, hyaline, 4-sp'd., no clamp connections. *Basidiospores* 6.5-8.0 (-9) x 2.5-3.5 (-4) µm diam (E_m = 2.41: E 1.62-3.00) oblong to oblong-elliptic, thin-walled, light brown in Melzer's solution and 3%KOH.

Habit, habitat and distribution: one very small cap found among the large bolete collection OKM 27200, on ground under ST-MF at 70m elev, above chicken farm, near Sabana Field Station, Luquillo, Puerto Rico, Jan 10, 1998.

Material examined: **USA**: **Puerto Rico**; near Sabana Field Station, Luquillo, Jan. 10, 1998. Coll. H.Miller OKM 27200 (VPI).

Observations: The single small specimen has spores which are distinctly smaller than any known species of *Phylloporus*. The spores of *P. rhodoxanthus* are 11-15 x 4.5-6 µm (Miller, 1973). In addition, the specimen has a very loculate hymenium and lacks the blue staining when bruised. More material needs to 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* "*savana*" which was fruiting all around this specimen. In the collecting site only two species known or suspected to be ectomycorrhizal in the low elevation tropical hardwood forest in Puerto Rico were found. These include *Hymenea courbaril* L. in the Caesalpiniaceae and *Andira inermis* (W. Wright) H.B.K. in the Papilionaceae (Lodge 1996) and the putative hosts were growing very close to where the fungi were collected.

Russula littoralis Pegler Mycotaxon 12: 93 (1980)

Pileus 3.8-~~6.0~~ 11.0 cm broad, broadly convex, plane with a shallow depression in the center, surface glabrous, moist or very slightly tacky over the margin, dull yellowish over the disc (Met 3A4), margin, olive-gray (Met 3C2-3), to brownish gray or tinted lilac over the outer one-half of the surface. *Lamellae* adnate, close to crowded, narrow, white, in age yellowish, ~~more~~ paler than

Pale Horn Color (2.5Y 8.0 8/3.5) 8 Glaucus 80 (6.5Y 5.90/1.2) to Cream Color (3.4Y 8.4/4.7 to Drab Gray (0.6Y 6.8 2.4;

4-5 mm broad, 1/mm at margin

(Met 4A 3-4), occasional long lamellulae and forking just at the stipe. *Stipe* 1.5-4.0(-5) cm long, 0.8-1.6 (2.8) cm broad, nearly equal to bulbous in one specimen, glabrous, dry, dull white. *Context* soft and pure white. *Taste* not distinctive. *Odor* not distinctive.

Sweet,

Pileipellus 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 x 7.5-20 µm diam with filamentous hyphae 3-7 µm dia. hyaline in 3%KOH, light yellow in Melzer's reagent. *Lamellar trama* of filamentous, to inflated, ovoid, to irregular cells 3-13 µm diam, thin-walled, hyaline in 3%KOH, yellowish in Melzer's solution. No clamps seen on any tissue. *Cheilocystidia and pleurocystidia* 50-78 x 8-9 µm diam, numerous lamprocystidia, narrowly clavate, subcapitate to mucronate apices, thin-walled, yellowish contents. *Basidia* 36-41 x 10-12 µm diam, clavate, thin-walled, hyaline, 4sp'd. *Basidiospores* 6.7-10 x 6-8 µm (E_m 1.15: E 1.0-1.33) subglobose, to globose, or broadly elliptic, thin-walled, with a small apiculus and small oval plage, small amyloid warts <0.3 µm solitary or partially connected by amyloid, weak low ridges. Spore deposit buff (Met 3A2).

British Virgin Islands: Guana I. land, 2 m elev; beach & veg. vegetation, under *Coccoloba uvifera* (in sandy soil), 24 Oct. 1997 D.J. Lodge G-103, Gua-17

Reagents: $FeSO_4$ negative; Gum-guaiac faint bluish; 2% Phenol negative.

N. Bay Woods Puerto Rico:

Habit, habitat, and distribution: in sand on dunes under Coccoloba uvifera, Piñones Commonwealth Forest, Beach near Loiza, PR, Jan. 14, 1998.

Material examined: **USA**: **Puerto Rico**; Piñones Commonwealth Forest, Beach near Loiza. Jan. 14, 1998. Coll. J. Lodge, O.K. & H. Miller OKM 27240 (VPI). add PR-3987, 3988 (VPI) from Piñones OAPR and maybe 3792 & 3892 from Mona Island, que

Observations: The species was described by Pegler (1980) from Grand Macabou, Martinique in sand under the "Seagrape, *Coccoloba uvifera L.*". This is the identical habitat in which we have found our fungus in Puerto Rico. The description of *R. littoralis* by Pegler from Martinique in the Lesser Antilles (1983) is close in every way to the material from the same habitat on Puerto Rico, Mona, and Guana Islands.

I need to see deposit

and Guana & Islands

Mona

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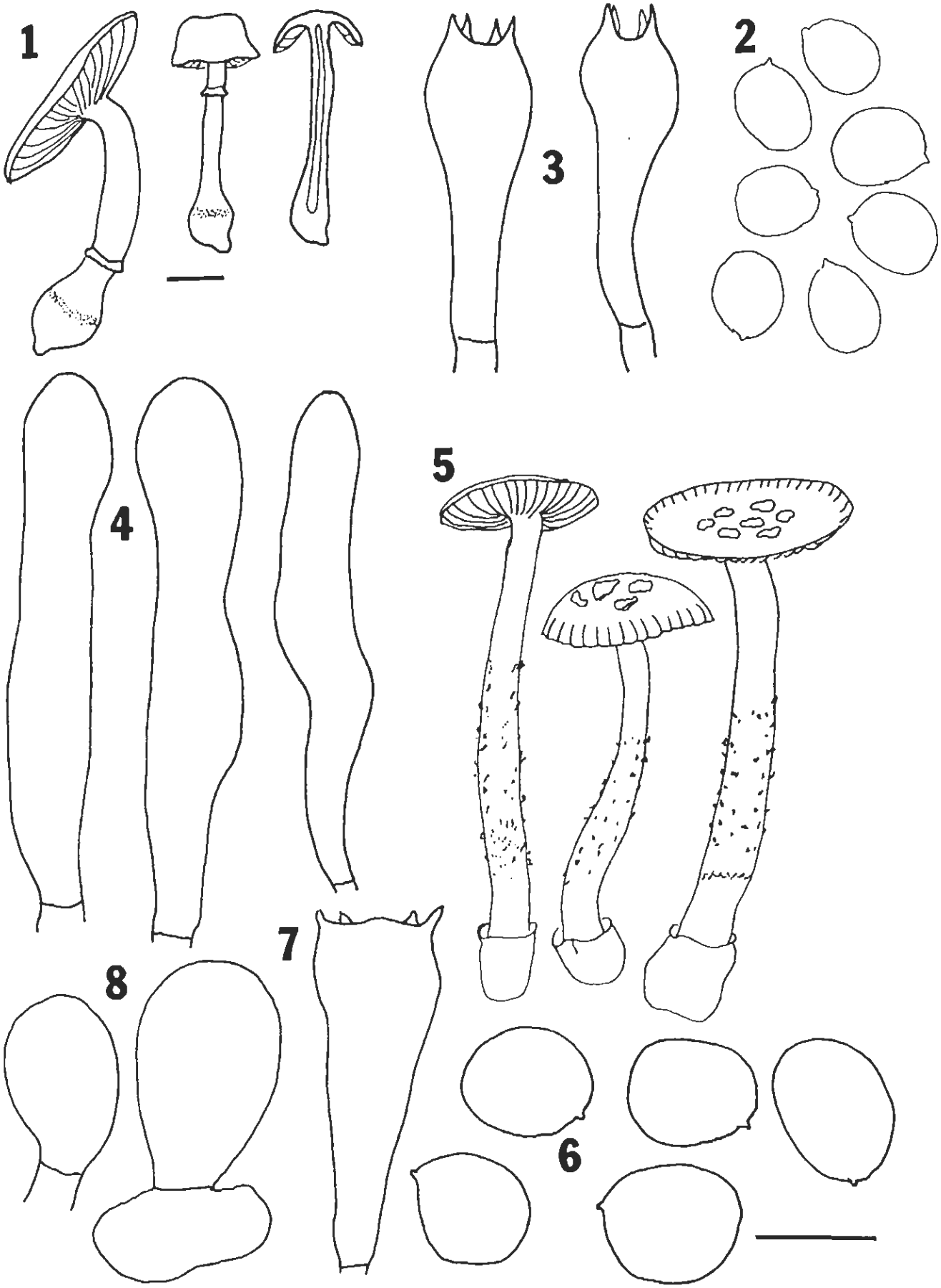
FIGS. 1-4. *Amanita cystidiosus* 1.Fruiting bodies. 2. Basidiospores. 3. Basidia. 4.Cheilocystidia. FIGS. 5-8. *Amanita albivolvatus*. 5. Fruiting bodies. 6. Basidiospores. 7. Basidium. 8. Cheilocystidia. Bar = 1 cm for FIGS 1 & 5. Lower bar = 10 µm for other FIGS.

FIGS. 9-14. *Lactarius coccoloba*. 9. Fruiting bodies. 10. Basidiospores. 11. Basidia. 12. Dermatocystidia. 13. Caulocystidia. 14. Cheilocystidia. Bar = 1 cm for FIG 9. Lower bar = 10 µm for other FIGS.

FIGS. 15-18. *Phlebopus* "*savana*" 15. Fruiting body. 16. Basidiospores. 17. Basidia. 18. Cheilocystidia. Bar = 1 cm for FIG. 15. Upper bar = 10 µm for other FIGS.

FIGS. 19-21. FIG. 19 *Amanita cystidiosa*. FIG. 20. *Lactarius coccobolus*. FIG. 21. *Phlebopus savana*. Bar = 1 cm.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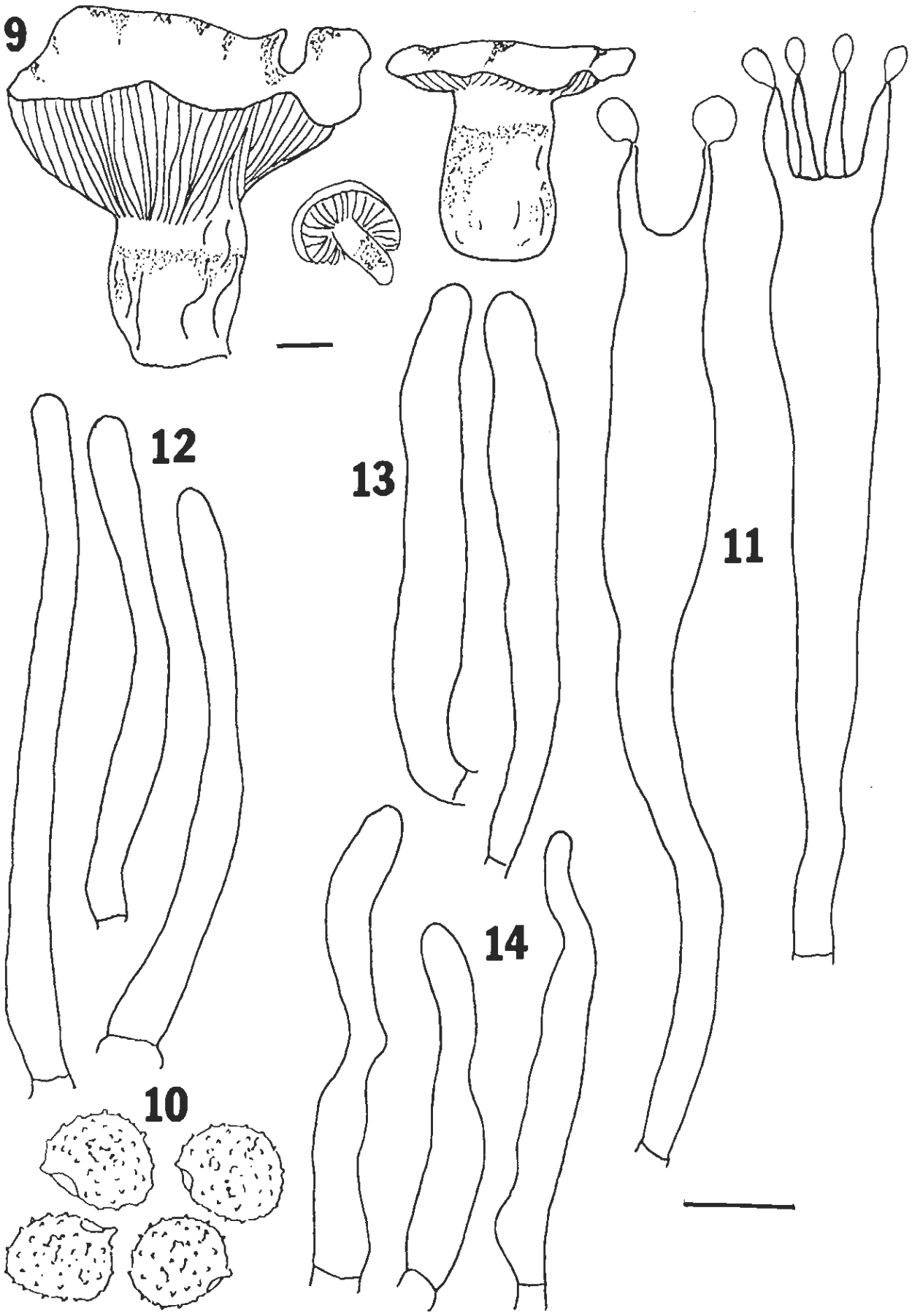
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Sombrero, northernmost of the Lesser Antilles proper, is today a tiny bit of oceanic limestone on a large bank, or submarine platform. The bank's edge, like all tropical island banks and continental shelves, is abrupt, at about 100 m below present sea level. At glacial maximum, as recently as 12,000 years ago, the whole bank was dry land. It is far from surprising that Sombrero has endemic species: it and its bank were never connected to any other land area.

No one thought Sombrero's unique species were "endangered" or needed legal protection because we thought there was nowhere else on earth anything could be safer. Ah, how wrong we were!

The prevailing winds at Sombrero are the northeast Trades and the prevailing ocean current sets westerly, into the Caribbean. The BVI are directly downwind and down current. At Cape Canaveral, Florida, the prevailing winds are westerlies and the current -- Gulf Stream -- sets northeasterly. On site catastrophes at Canaveral are contained by a vast and intricate system of drains and settling pools, surfacing several square miles of marshland -- in itself an environmental buffer. In-air catastrophes at Canaveral deposit their chemicals, pieces, and schoolteachers well offshore, on a route that takes them away from human habitation. Anything and everything bad that might happen at Sombrero comes to the BVI.

I have culled and excerpted the now copious correspondence and literature on the proposed rocket launch facility for Sombrero. I visited Anguilla in March and talked to the main players resident there. I visited MCZ subsequently and re-examined the only extant two (2) specimens on the Sphaerodactylus gecko I collected in 1963.

In the bottle with the specimens is a pencil note in the handwriting of the late Benjamin Shreve, in the '60's the world's foremost authority on Sphaerodactylus. He opined that these two individuals represent a new species but that he would not describe it without more -- and adult -- specimens: both are juveniles. This is very reassuring, and he spells out the ways they are distinctive. Still, I agree with Shreve: more specimens, including adults. (The same can be said for the Carval Rock, BVI, form we got two of last year.)

If I have a role in all this, it will be to describe and name the new gecko, or find someone else and at least oversee that process. I would need modest funding for this, if and when people in the field get the specimens. Meantime, concerted effort should be brought to defeat the Beal proposal: it is a bad deal for reasons far more pragmatic than rare, endemic lizards. Note my last bit, suggesting it may simply be a scam. I hope so.

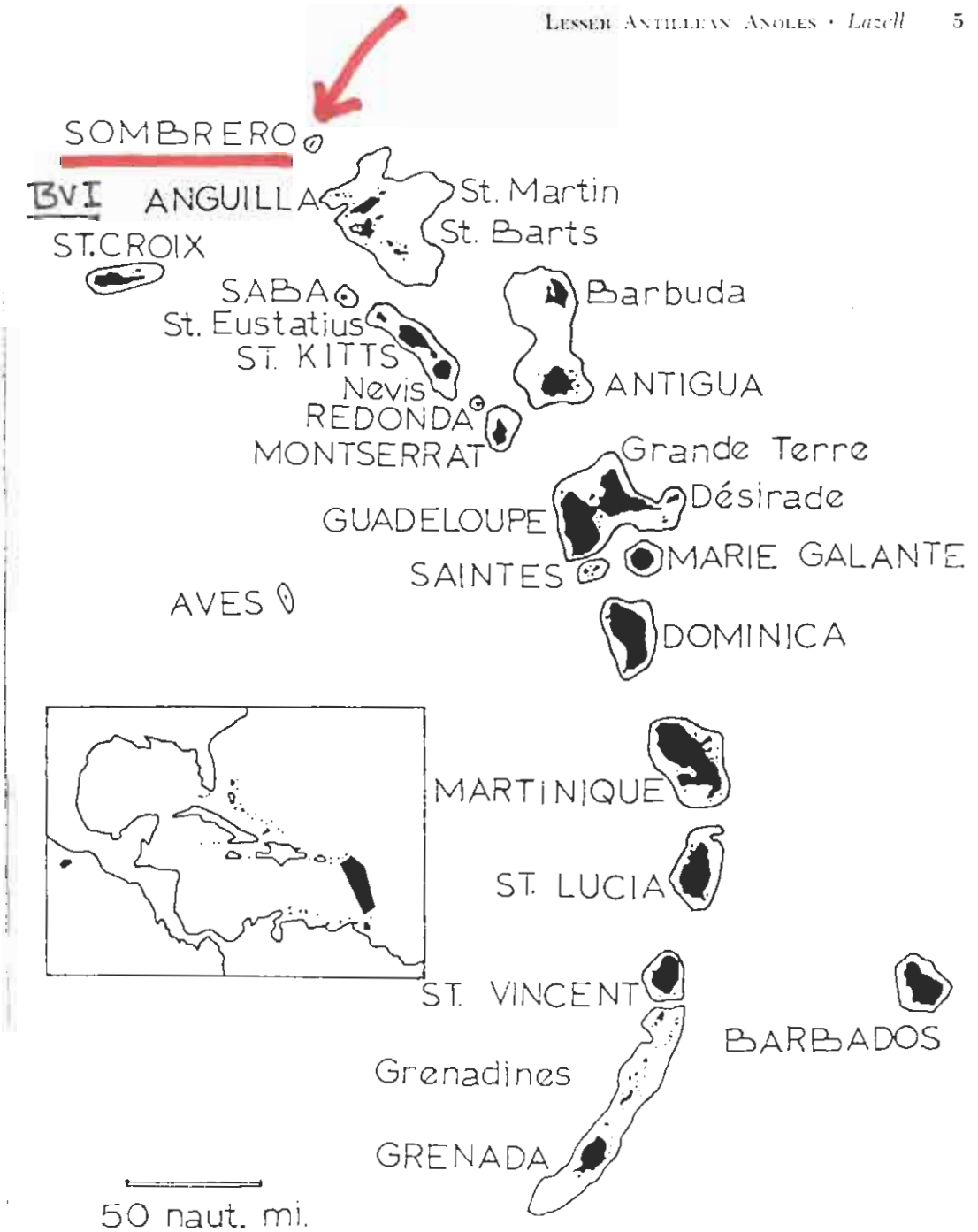

Figure 1. The Lesser Antilles. Approximate bank borders are indicated. Banks are named for their largest island (capitalized). The inset shows the position of the Lesser Antilles (black) relative to the other land areas of the Caribbean Basin. [illegible] (unshaded).

Caribbean Spaceport

By JAMES ANDERSON

SOMBRERO ISLAND, Anguilla, May 2 (AP) -- It's an audacious plan: Take over a desolate, wave-battered Caribbean island, launch commercial satellites and make a lot of money.

That's Texas entrepreneur Andy Beal's vision for Sombrero Island, a crusty patch of rock and limestone that is the first sight of land for many ships approaching the Caribbean from Europe.

Skeptics question the site choice. Over the years, rough seas and insistent salt spray have flattened boulders, carried away tombstones and destroyed buildings from a 19th century mine that shipped phosphate to farmers in the U.S. Midwest.

And Sombrero's brittle coral rock is pocked with pits exposed to water below -- hardly ideal for a launch pad, critics say.

Beal Aerospace Technologies Inc. says Sombrero will work fine as a site to join the $50 billion commercial space industry. It plans to build a spaceport for a three-stage, 223-foot rocket similar in size to the European Space Agency's Ariane 5.

Officials see a windfall for Anguilla, a British territory of 10,000 people dependent on tourism. The local government has agreed to a 49-year lease of Sombrero, 38 miles north of Anguilla, if Britain approves.

But opponents, including Britain's influential Royal Society for the Protection of Birds, say Sombrero is a key nesting ground for Caribbean seabirds, including the masked booby.

They ridicule Beal's offer to find another bird sanctuary.

Beal's plan also has pitted Anguilla's government against those who warn that rocket launches would chase away tourists seeking peace.

"God help Anguilla if they decide to go elsewhere," said a former chief minister, Sir Emile Gumbs.

But the current local government chief, Hubert Hughes, contends many critics are wealthy expatriate landholders -- white Americans and Europeans among an overwhelmingly black population that earns on average about $7,300 a year.

"They have this attitude that the island shouldn't develop because they have come to live a quiet and peaceful life in their tropical paradise, in their little castles, and they don't see finding jobs for the people of Anguilla as a priority," Hughes said.

More than 50 commercial satellites were launched in the United States alone from 1995 through 1998, and most spaceports worldwide are booked.

Enter upstart Beal, created in 1997, which considers Sombrero ideal. A launch pad near the equator makes it easier to put payloads in certain orbits, it says. With open seas all around, launches won't endanger human settlements, Beal says.

British Virgin Islanders, however, question whether rocket exhaust and fuel spills could reach them 65 miles away.

Currently in development, the Frisco, Texas-based Beal's BA-2 rocket is designed to carry 13-ton payloads. Its first test launch is set for December 2000.

Ultimately, Beal plans 12 space shots annually in a market that charges $75 million to $125 million a time.

The company wants to pave over less than 10 acres of Sombrero's 90 acres for a launch pad, fuel storage, control buildings and airstrip.

Finance Minister Victor Banks said it could make Anguilla $6.1 million a year -- one-fifth its current budget -- including the lease starting at $280,000 a year.

"Here is an opportunity to do something with an island that has no value," Banks said.

Robert Harris, Britain's governor on Anguilla, said that Beal's technology appears sound and that a review might be completed by year's end.

"If Britain isn't satisfied, then the thing's not going to be built," Harris said. "Indications are that that is not going to be the case."

Sombrero's only residents, a handful of lighthouse keepers who spend weeks alone, consider Beal's vision for "The Rock" with disbelief.

Only by scrambling inside the lighthouse, perched atop 40-foot cliffs, did they survive hurricanes that have periodically swamped the island.

Beside the June-to-November hurricane season, "ground seas" reaching 60 feet can pound Sombrero. Lesser seas can stop boats from landing, sometimes for weeks.

A Beal vice president, David Spoede, said, "We'll work around the weather in terms of launches."

Anguilla's National Trust is trying to come up with an alternative use for the island. With its aging buildings and tombstones, old lighthouse and mining equipment, some say Sombrero is a ready-made museum.

"It really comes down to our cultural heritage," said the trust's executive director, Ijahnya Christian.

Banks, the finance minister, said few Anguillans seek out that heritage. "I think that 95 percent of the people of Anguilla have never seen Sombrero," he said.

From: Michael A. Ivie, Ph.D. <mivie@montana.edu>
To: Bruce Potter at Island Resources <bpotter@irf.org>; epaul@dclink.com <epaul@dclink.com>
Cc: caribbean-biodiversity@egroups.com <caribbean-biodiversity@egroups.com>
Date: Monday, March 01, 1999 5:43 PM
Subject: [caribbean-biodiversity] SOMBRERO: Responses to Beal's Statements

>Hi Folks, it's Grumpy here with a rant.
>
> I hate being right when it is a pessimistic prediction, but I >warned that the bird wonks wouldn't be able to argue this case, and that >relying on bird data would be disastrous. Frankly, Beal is ABSOLUTELY >CORRECT: there is nothing about the specifics of the seabirds nesting on >Sombrero that is unique or particularly worthy of protection. In fact >the stupid situation is that, from the arguments they have been given by >the bird protectionists, Beal could conceivably decide to help the >seabird population by wiping out the ground lizard that eats their >eggs!!! Yet it is mainly the lizard that is in fact, unique and worthy >of saving. Yet the birders were so blind that they put their money into >sending birders out to document yet again that there is nothing >ornithologically unique about Sombrero!
>
> In my opinion, the bird angle should be completely dropped except as a >fund-raiser, and use the money to get people who know Caribbean >biodiversity onto Sombrero, i.e. people that can do something to save >it. Seabirds are Sombrero's equivalent of green plants for most >habitats, they deliver energy to the native ecosystem. Beyond that, >they are just another batch of widespread, non-endangered birds. Legal >protections will never fly based on the birds. As the main energy >transfer system of marine calories to a terrestrial community with >precious little in the way of energy fixing plants, they are a critical >driver of the system. The problem is, Beal can save the driver, and not >the parts of the system that are unique.
>
> Why isn't the ground lizard on the IUCN Red List? Because no one >thought anyone would be crazy enough to mess with Sombrero. Secondly, >why haven't the bird folks, who are only ones who can raise the funds, >sending botanists, herpetologists, and entomologists out there to find >endemic species worthy of legal protection, and that will stand up in >court challenges? (Bats are another possibility, if a long shot) If >they want to save the birds, they need to look to the smart path, not >the familiar one.
>
> The Beal folks are probably well-meaning, after all they belong to such >organizations as "Greenpeace, the Sierra Club, the World Wildlife >Federation, the Royal Society for the Preservation of Birds" -- i.e. >well-meaning and blissfully ignorant of how the natural world works. We >have to educate them, not feed them drivel about pretty birds. Beal has >responded in a manner totally appropriate to the data they were >delivered, so shoot the messenger, not the recipient. The situation so >far is not that far removed from wanting to stop the replacement of a >bridge because starlings like to roost on the old one.
>
> Now, this is not to say the Beal folks are particularly smart, since >who would want to build a satellite launch pad in a place they claim >gets totally over-washed with sea water during periodic hurricanes?
>
> OK, how to proceed. First, redefine the role of seabirds on the island >in terms of energy delivery to an isolated and fragile terrestrial >system. The unique ground lizard is the top predator in this system, >the equivalent of the wolf, killer whale or grizzly bear of Sombrero. >This is the poster-child for protection, especially in the legal sense. >It is found nowhere else on earth, and as such is eligible for >protection under the IUCN endangered list. Britain, as an IUCN and Rio >signatory, has certain treaty responsibilities to protect this species >(unlike any of the widespread, non-endangered birds that nest there). >However, it is probably not the only unique species, but without the >resources to look for them, we can only surmise. Note that any system >that can evolve such a unique large vertebrate top predator (OK, large >on my scale) must have a whole system that is unique, including many >invertebrates that have evolved to directly utilize the guano and dead >birds that are delivered by seabird visits, as well as the few >established green plants. Just like the lizard, there must be unique >predators that have evolved among the terrestrial invertebrates to feed >on these endemics, and so on. The hatchling lizards almost certainly >live on insects until they are big enough to take eggs, and perhaps also >between nesting seasons.

> I am sure that Lianna Jarecki and others will provide extensive reasons
>why the claim that jet fuel and H2O2 (among other obvious things) cannot
>be considered inconsequential to the marine environment in the event of
>an accident, especially given that Beal claims the entire island is
>subject to periodic overwash. The fact that such obvious arguments must
>be made indicates that this whole thing will have to end up in the
>courts. As such, real data on unique biodiversity MUST be obtained in
>order to win. The bird data won't do it, and the better the bird data
>(by itself) the more evidence Beal will have that they are hurting
>nothing unique.
>
> Again, if someone can arrange it, I am available to do an insect
>inventory of Sombrero, and we all know how to find the lizard, plant and
>bat people we need. It is just a matter of finding the transportation
>money -- no salary, no supplies, just travel expenses.
>
>Mike

JCINJTOWN@aol.com wrote:
>
> Hi All,
> Mike Ivie is spot on absolutely right. The whole ecosystem is remarkable
> and no doubt has more endemics. No one ever mentions the Sphaerodactylus
> gecko, known from just two (2) specimens but quite distinctive. The taxonomic
> climate of the times (1964) precluded formal naming but with cladotaxonomy
> today it would easily qualify as a new species. I have been to Sombrero
> (sadly but certainly no bats) and do not need to return. All I need are a few
> more of those geckos. Entomologists looking under things will find them.
> Please send me some at MCZ, Harvard, 26 Oxford St. Cambridge Mass 02138,
> USA
> Thanks, Skip (Dr. J.D.) Lazell
>
>

Skip, many thanks for sending your Sombrero and Aves papers. So YOU are the source of Beal claiming the birds are being decimated by the lizards! :)

I'm waiting for Sir (formerly Captain) Emile to get me some specimens, including the mouse, which no one has really examined to see if it's the common field mouse found here or some new mus sombrericus.

Best regards...

Bob Conrich
Anguilla National Trust

> Bob, I just talked to Ellen, 8.iii.99. She found Sphaero onSombreo after the
> hurricane, but did not collect. She does not want to describe it even if more
> specimans are available. I have 200+ publs and do not need more, so anyone who
> wants to describe the Sphaero is welcome to it. To proceed, get a team of
> entomologists on Sombrero with instructions to catch some.

Skip

THE REPTILES OF SOMBRERO, WEST INDIES.—The tiny cay of Sombrero forms the northern limit of land in the Lesser Antilles. It lies some 32 miles northwest of Anguilla and on a separate bank from that which includes the numerous islands from Dog Island (and Anguilla) southeast to the Ile Coco (and St. Barts). To the westward, Sombrero is separated from the Puerto Rico bank (and Virgin Islands) by the Anegada Passage, the geographic and geologic border of the Lesser Antilles proper in the north and west.

Sombrero must have originally been volcanic, though, as a "second cycle" island of Davis (1926, The Lesser Antilles, Map of Hispanic America, *Am. Geog. Soc., Publ.* No. 2:41), it has been capped with oceanic limestone. Today, the cay itself is about ¾ mile long and 400 yards wide at the widest part; it is oriented roughly north–south. Sombrero is a block of oceanic, "honeycomb" limestone; it is from about 20 to 40 ft high and cliffed on all sides. There is no beach or strand. There is no tree, bush, or shrub anywhere on Sombrero.

The top of the island is table-like except for numerous pits, both natural (from wave erosion) and man-made (from phosphate mining). There are a few scraggly clumps of cactus (*Opuntia*). Other than these, the extremely sparse vegetation consists of a few tiny, ground-trailing, herbaceous plants, the commonest referred to as "camphor," and a half-dozen small weeds. The best detailed description of the island to date is that of Julien (1806, *Trav. Environ Nat. Hist.* 8: 1–28).

For over 100 years, the British government has maintained a lighthouse on Sombrero, and, because it lies at the mouth of the Anegada Passage, probably as much tonnage of shipping passes within sight of it as passes any island in the West Indies. Nevertheless, it is apparent that very little collecting had been done on Sombrero until I went there on 1 June 1963.

In 1960, the lighthouse which had stood for a century on the rock was swept away by a hurricane which is said to have completely covered the island with water. The new lighthouse has been operated by a crew of 4 men and supplied from Anguilla by schooner on the first and fifteenth of every month.

The lack of zoological exploration is revealed by the fact that only a single living reptile, the endemic ground lizard *Ameiva corvina*, has been known to occur there. Indeed, Darlington (1957, Zoogeography: the geographical distribution of animals, John Wiley & Sons, New York) cited Sombrero as an extreme example of the correlation between island size and number of species occurring on oceanic islands (p. 483), following Cope (1861, *Proc. Acad. Nat. Sci. Phila.* 1861:312–314) and Dunn (1934, *Copeia* 1934 (3):105–111), who believed that only a single reptile existed there.

Of course, Sombrero does support a large colony of nesting sea birds. When I was there the following species were breeding: *Anous stolidus, Sterna anaethetus, S. fuscata, S. dougalli, Gelochelidon nilotica*, and *Sula leucogaster*. In addition, *Phaethon aethereus* was seen, and presumably breeds in holes in the cliff face.

There are apparently no mammals or amphibians established on Sombrero, but the following reptiles were collected:

Ameiva corvina Cope (MCZ 76940-7).—This is a large, short-headed, heavily built *Ameiva*. Like many other ameivas, this form is somewhat skittish; it is easily collected, however, by the expedient of attracting individuals' attention with eggs. By merely throwing an egg near an individual it may be easily noosed, as it will usually become engrossed in lapping up the splattered egg rather than watching the collector. I used 2.5-foot sections of a bamboo fishing pole and a fine wire noose.

Certainly, the greater portion of the diet of *Ameiva corvina* is bird eggs. The lighthouse crew reports that nests and eggs can be found on the island during at least 8 months of the year. I was there at the height of the breeding season, and at that time the ameivas had tails greatly distended with fat—appearing medially swollen and basally constricted. The ameivas are both stolid and aggressive with respect to the nesting birds. They will wait patiently for a bird to leave the nest,

then dart in swiftly, smashing the egg and lapping up its contents before the bird can return to drive them off. Large individuals often crack an egg enough to get a mouth grip on it, then carry it away from the nest. As anoles go, *A. corvina* seems to be a good climber, scaling the pitwalls both for bird eggs and basking ledges. The species is abundant all over the island.

In life, *Anolis corvina* is slatey black, the males becoming distinctly browner on the head. The venter is mottled with light blue, and often has a green cast; in some individuals green speckles extend boldly onto the tail. Some males show brown flecking on the dorsum; females appear darker generally than males.

Anolis gingivinus (MCZ 75581-7).—This form has been regarded as a subspecies of *Anolis bimaculatus* by Underwood (1959, *Bull. Mus. Comp. Zool.* 121:5). Williams (1962, *Bull. Mus. Comp. Zool.* 127:9) doubted conspecificity, and I find it untenable. *A. gingivinus* differs strikingly from *A. bimaculatus* (a species of the St. Kitts bank) in color, pattern, size, development of the throat fan (which is nearly vestigial in *bimaculatus*), and in number of subdigital lamellae under the second and third phalanges of the fourth toe (18–22 as compared to 28–36 in *bimaculatus*).

Anolis gingivinus is the common anole of the Anguilla bank, occurring from Dog Island (MCZ 75566-75) to the Ile Coco (MCZ 75630-4) on every rock or cay that has so much as a single bush or shrub. In contrast with the observations of Auffenberg and King (see Williams *op. cit.*), I found *A. gingivinus* closely associated with trees, bushes, and shrubs everywhere throughout its range except on Sombrero. On Sombrero, *A. gingivinus* is fairly common on the ground and in stone heaps all over the island. Individuals were very skittish compared to any seen on the Anguilla bank, and were often found beneath rocks.

In life, *Anolis gingivinus* varies from the usual olive drab to distinctly light greenish, or even tinsy, in ground color. The venter varies from cream to bright yellow, and is brighter, as a rule, in females. The throat fan of males is well developed and yellow-orange in color, with white scales. Color change is merely to darker, enhancing the gray-brown pattern; greener individuals turn browner. The pattern consists basically of a very broad middorsal band, which may be darker or lighter than the ground color in the same individual at different times, and a bold, light flank stripe from shoulder to groin. In males, this pattern is often modified by inclusion of spots or marbles of grey-brown. In individuals from Sombrero, there are from 1 to 3 large, oval spots in the costal region immediately lateral to the middorsal band. This pattern variant occurs in a small percentage of Anguilla bank populations (10–20% in St. Martin or Anguilla, for example).

Taxonomic recognition of a population that, though it assuredly differs on an average, could only be defined by characters included within the range of variation of other populations of the same species is, in my opinion, pointless. The average differences seen between Sombrero anoles and their relatives on the Anguilla bank, like similar average differences between populations on that bank, are excellently explained by the "founder principle" as set forth by Mayr (1963, Animal species and evolution, Harvard Univ. Press, p. 211).

The differences in habitat and behavior that seem to obtain so strikingly between *gingivinus* from the Anguilla bank and those from Sombrero are of greater interest. It is possible that this anole has been recently introduced to Sombrero. If so, it has been able to adapt to conditions there considerably more austere than those in which it lives elsewhere in its range; this behavioral and habitat adaptation could be antecedent to discernible changes in morphology, e.g., toe lamellae. It is not impossible that the Sombrero anoles may provide a rare opportunity to observe and document geographic speciation throughout its stages and processes.

Sphaerodactylus near *sputator* (MCZ 73856, 74340).—On Sombrero, this tiny gecko is difficult to collect because of the porous substrate. I saw the species at the north end of the island, but both specimens collected were taken beneath boards and stones not far from the lighthouse. The lighthouse crew reported that sphaerodactyls are often seen on the surface during rainstorms, but all those I observed were well beneath fair-sized objects.

It is again possible that this species has been recently introduced to Sombrero by boat, though I find it very difficult to believe. *S. sputator* is the common sphaerodactyl of

the Anguilla bank, and occurs as well throughout the St. Kitts bank. Although King (1962, *Bull. Fla. State Mus.* 7:1) does not record specimens of *S. sputator* from Anguilla itself, his suspicion that is occurs there has been substantiated by the collection of specimens just north of Sandy Ground (MCZ 74388–9) by me. At least on the Anguilla bank, this form may be collected in areas closely similar to Sombrero.

All Sombrero individuals seen were at or near the longitudinally striped extreme color pattern figured and described by King (*op. cit.*). The dorsal scales of Sombrero specimens appear smaller (counts 45 from axilla to groin) than in specimens from the Anguilla bank islands.

The discovery of *Anolis gingivinus* and *Sphaerodactylus* near *sputator* on Sombrero not only triples the number of known species of living reptiles from the island, but also demonstrates the presence of at least 1 representative of *Anolis* on every bank of islands in the Lesser Antilles. The other widespread and abundant genera of amphibians and reptiles in the Lesser Antilles (*Eleutherodactylus, Alsophis, Dromicus, Iguana, Ameiva, Hemidactylus,* and *Thecadactylus*) apparently have not been able to equal this achievement.

I am most grateful to Mr. V. F. Byron, the Warden of Anguilla, and Commander T. A. Pack-Beresford, Inspector of the Imperial Lighthouse Service, for their friendly cooperation in swiftly shearing all official red tape connected with my trip. Especial thanks go to Captain Emile Gumbs of the WARSPITE, who provides regularly scheduled transport to Sombrero that is free of charge to passengers. Mr. H. E. Richardson and his family, of Sandy Ground, Anguilla, made pleasant and comfortable my stay on that island. The expedition that included my trip to Sombrero was supported by National Science Foundation Grant G-16066.—JAMES D. LAZELL, JR., *Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.*

> Dear Friends
>
> Concerning the Beal project for Sombrero, a little history may be appropriate. It is
> also all that my limited expertise allows me to contribute to the present discussion.
>
> There is reported in the English volumes of law reports, at 3 Appeal Cases, page 1218,
> an interesting decision of the House of Lords in 1878. The case is known to all company
> law students as Erlanger v The New Sombrero Phosphate Company. Sombrero had been leased
> in 1865 to The Sombrero Company for L1,000 a year to work the beds of phosphate found on
> it. The company had exploited the resource, and on exhausting the mineral deposit and
> ceasing business had been ordered by the Crown to be wound up. In 1871 the remainder of
> the lease was purchased by a syndicate, of which Erlanger, a banker, was the head. They
> paid L60,000 for it. The syndicate floated a joint stock company to sell shares to the
> public to purchase the lease from the syndicate. They claimed that the new company would
> work the minerals on the island. Immediately after purchasing the lease, they sold it
> to the new company which they had formed for the purpose: the New Sombrero Phosphate
> Company. The purchase price was L110,000, which at that time was a very great deal of
> money.. After a year or two, no phosphate having been exported and no progress being
> made, the shareholders appointed investigators. A quick visit to Anguilla and Sombrero
> revealed that the project was not feasible, as the object for which the company had been
> formed was an impossibility. The phosphate had long been exhausted.
>
> Returning to London, the detective made his report, and a suit was brought against
> Erlanger and his banking and financial collegues. The promoters had kept out of the
> prospectus, and hidden from the 496 shareholders, the details of the contract and the
> fact that the promoters were personally to benefit from the sale of Sombrero to the
> company. In the High Court, the Court of Appeal, and the House of Lords, the judges
> agreed that the contract could not be allowed to stand. The promoters of the company
> had misused their powers to advance their own interests and not that of the company.
> The fact that Erlanger's syndicate included an Admiral of the Fleet and the Lord Mayor
> of London did not prevent their Lordships from holding that the extent of mala fides, or
> lack of good faith, in the contract with the company entitled the company to set aside
> the contract and to get its money back.
>
> This case is the foundation of the common law duty of promoters to disclose in the
> prospectus any profit they hope to make from any contract with the proposed new
> company. The case is well known to every British, Canadian, Australian, West Indian and
> US company lawyer. Might Mr Beal have heard of it and been tickled by the challenge?
>
> Assuming that Mr Beal intended to make a great deal of money from this project, is it
> possible that he has never intended to place a bag of cement on Sombrero?
>
> There is an expression, Plus ca change, plus c'est le meme chose. The phrase deja vu
> also flashes by. On the other hand, this may all be paranoid suspicion on my part and
> an unworthy comparison of Mr Beal with Baron Erlanger. Beal may well have figured out
> how to land giant rockets on Sombrero through 40 foot high ground seas, and to maintain
> them to launch through the corrosive sea blast that characterizes Sombrero.
>
> Best regards to all
>
> Don Mitchell, QC
>

Subj: **Re: Anolis work, July 1999**
Date: 04/16/1999 10:59:30 AM Eastern Daylight Time
From: clivep@caribsurf.com (Clive Petrovic)
To: gad_perry@compuserve.com (Gad Perry), lutch@caribsurf.com (Dawn L)
CC: razdmiel@post.tau.ac.il (Razi), jcinjtown@aol.com (Skip)

Dawn, Clive, et al.,

Skip tells me things are looking good for our project this summer, which is great. So, I thought this would be a great time to make sure we are all on the same page in terms of what, where, and when.

Let's start with the What. I think we decided on three populations: Sage Mountain for the wet extreme, Necker Island for dry, and Parquita Bay for middle ground. We said 15 each for the two extremes and 10 for the College beasts, which we can easily replace if need be from local stock. So we need 40 cages. I think we said each would be 1X1X2 feet.

Now, to the Where. We talked about the College grounds, probably under the big tree near the new building containing the SCUBA gear. We planned on using one of the rooms in there for measurements and building some kind of table system to hold up the cages outside. I believe the equipment is all in Liana's lab, though the balance may be on Guana in storage in Henry's house somewhere.

Finally, the When. Ideally, I'd be coming over on the first week of July. The basic setup would be ready by then, and Dawn and I would spend the week catching the lizards and setting everything up. Dawn would then be in charge of taking care of the lizards (initially watering, and feeding ad lib throughout) and taking the water loss measurements, at least once a month for each animal, until we get there in October. If she can make more frequent measurements during the summer, when she's on break, great - but not essential. This will give us about 3.5 months of data. I think Razi and Dawn have talked about the specific schedule of measurements.

OK, assuming this is all correct, here's what I think needs to happen:
- 40 cages and their support structures need to be built by 1 July.
- the lab space needs to be allocated and equipment organized and set up
- lizard food needs to be sent over and kept alive
- travel arrangements (flights, boat day, access to Necker) need to be made.

The first two items will fall on the home team, Dawn and Clive. I can send crickets and/or mealworms, assuming there is some place to keep them. I suspect Skip is going to need to arrange final permission for the boat day and Necker access, and other travel arrangements are mine to make. So, if everything above is correct - and we should definitely correct anything on this that is not - and I haven't forgotten anything important, the question is: Do you still think these can all be arranged in time? My end of it is easy enough, but the job for the home team is pretty complex and time-consuming. Let's be realistic - it is better to call this off than to go to all the trouble and expense and only have a half-baked half-project that tells us little. Are we Go?

Gad

Gad,
Good to hear from you. I think it would be great to get the project going this summer. I believe most of the logistics would be the same as last year. Outside space, lab space, equipment etc should be available as last year. The equipment is still in the box in the biology lab.

The only potential problems (could be serious) revolve around my schedule and possibly Dawn's for the summer. I will be gone all of May and for other periods during the summer. During July and August I should be here most of the time. There is an OECS project that may take me away from Tortola for about three weeks in August. Otherwise I can be fairly flexible. I have not had the opportunity to discuss this in detail with Dawn. I know she was considering various options for the summer. Obviously her availability is critical unless we can find someone else to fill in. Lianna may have a biology student interested in participating. All this needs to be worked out before we can make a final plan. I would very much like to see the project move ahead and am willing to do what I can toward that end.
Clive

Hi

I got all your messages..... I am planning to be available for July and August..... I may not be here in September..... so we will need to talk about that..... It would be nice to have some assistants..... although I know I will need to do the bulk of the work.... which I am prepared to do.....

I am hoping to meet with Clive... to talk more about the project.....

Thanks for keeping in touch.

Dawn.

Biomass Plots

The four 100m² biomass plots that were cleared to bare ground were re-examined on 1 May 1999. Vegetation on all has rebounded well -- almost too well to now use them experimentally. Bent feels strongly that tam-tam retards other species by usurping all the water. George and I had not considered this; we just noticed tam-tam was eventually over-topped by sea-grape, Tabebuia, etc. So, an experimental opportunity arises.

As of now, here is how the plots look:

Plot 1, originally old tam-tam, is now dense, meter high tam-tam over bur weed. I would brush-hog this out in October and plant saplings of good stuff from Lianna's nursery: sabal palm, Tabebuia, etc.

Plot 2, originally sea grape and Tabebuia just beginning to over-top old tam-tam, is recovering pretty much that way. the good stuff has stump-sprouted and is just out-distancing the tam-tam, which is also meter high. I would plant several young sabals, or -- even better -- royal palms, here, but cut nothing.

Plot 3, originally young tam-tam, is just that again, only lower (of course) than the surroundings. Here I would plant all the same good things we put in Plot 1, above, but without brush-hogging out first. Now we have a comparison that can test Bent's hypothesis.

Plot 4, in the White Beach strand woods, is already experimental: one half is fenced, one half unfenced, and an area equal to one half (i.e., 50 m²) that was not cleared has been fenced as a control. The three plots are very different. The unfenced, cleared one has excellent, stump-sprouting, broad-leafed saplings (don't know species) and a big papaya. The fenced, cleared piece has lots of little

papayas, no big ones, but excellent sea grape recovery. The control (fenced, uncleared) has lots of big ground bromeliads. The significance, etiology, cosmology, and metaphysics of all this escapes your correspondent who, confounded by nature, shall repair to books (or, better, ask a botanist).

Someday, but probably not in 1999, I want Gordon and Renee to come back and do one more plot in the North Bay woods because that is where I have my best Sphaerodactylus pit-trap density data.