



# OCCASIONAL PAPERS

## PRESENCE OF *STENODERMA RUFUM* BEYOND THE PUERTO RICAN BANK

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### ABSTRACT

Until now the red fig-eating bat, *Stenoderma rufum*, had been known only from the Caribbean islands of Puerto Rico, St. Thomas, and St. John. The capture of one specimen on St. Croix is noteworthy because this is the first reported capture of this species beyond the Puerto Rican bank. The female captured was post-lactating and pregnant, suggesting this is not an isolated individual, but a breeding population on St. Croix is more likely. St. Croix's distinct origin and independence from the northern Virgin Islands indicate *S. rufum* most likely arrived by over water dispersal to St. Croix from adjacent islands (St. Croix is 68 km south of St. John and St. Thomas and 101 km southeast of Puerto Rico). When morphological characters and habitat characteristics are compared between the St. Croix *Stenoderma* with female *S. r. rufum* from St. Thomas and St. John and *S. r. darioi* from Puerto Rico, none clearly align the St. Croix specimen with either subspecies, except pelage color is consistent with *S. r. rufum*.

Key words: cranial characters, external morphology, St. Croix USVI, *Stenoderma rufum*

### INTRODUCTION

The red fig-eating bat, *Stenoderma rufum*, is known from the Caribbean island of Puerto Rico and the northern United States Virgin Islands (USVI) of St. Thomas and St. John (Fig. 1) but not from the southern USVI of St. Croix (Hall and Bee 1960; Hall and Tamsitt 1968; Genoways and Baker 1972; Koopman 1975; Timm and Genoways 2003). *Stenoderma* was first described by Étienne Geoffroy St.-Hilaire (1818) as "le *Stenoderme roux*" based on a single specimen, the type locality not known, but it originally was believed to have come from Egypt. Since the one known specimen resembled New World bats rather than bats known from Egypt or the Old World, Demarest (1820) used *Stenoderma rufa* in his original description and

the type locality indicated as "unknown" due to its doubtful origin. When Peters (1869) visited the Paris Museum and examined the type represented by a damaged skin and no skull, he was deceived by the faulty figure of Geoffroy and named the bat a *Vampyrops*. Peters (1876) subsequently examined the type of *Artibeus undatum* Gervais (skull only, skin thought to be lost) in the anatomical collection at the Paris Museum. The similarity of the skull of *A. undatum* and the skull figured by Geoffroy led Peters to conclude the skull of *A. undatum* was actually the missing skull of *Stenoderma rufa*. This established the identity of the species, but not its habitat. The supposition that the genus and species would be rediscovered in the West

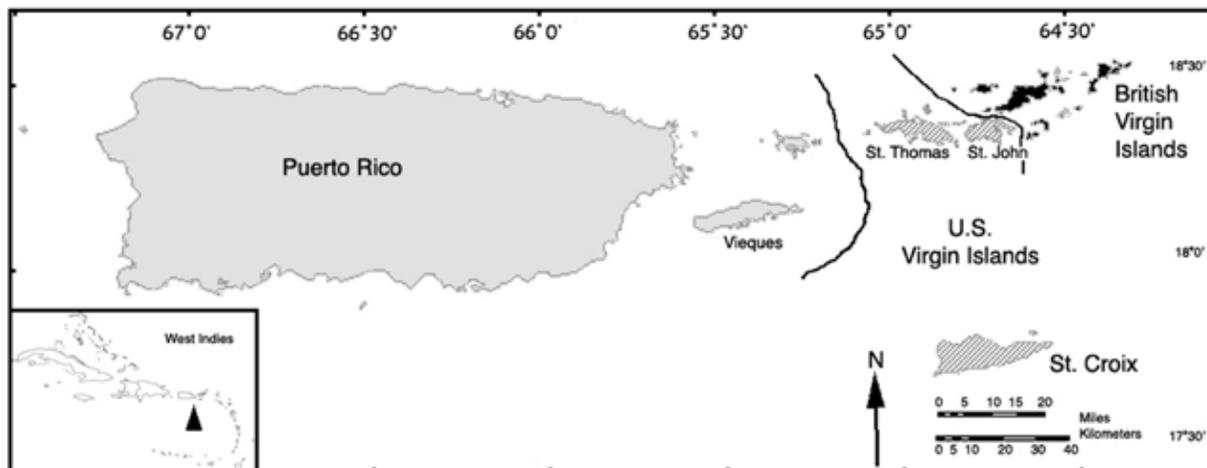


Figure 1. Current geographic distribution of *Stenoderma rufum* in the West Indies includes *S. r. darioi* from Puerto Rico and *S. r. rufum* from the United States Virgin Islands of St. Thomas, St. John and St. Croix. The inset map and its arrow approximate locations of Puerto Rico and Virgin Islands in the West Indies. The United States Virgin Islands (slanted lines) are defined by the boundary lines to their west to distinguish their territory from Puerto Rico (grey) and to the east to distinguish them from the British Virgin Islands (black).

Indies was accepted by scientists studying American Chiroptera (Allen 1911). The distribution and status of this taxon remained quiescent until Anthony (1918, 1925) discovered sub-Recent fossil remains in caves of Puerto Rico. No additional living specimens were collected until 1943, when Harry A. Beatty obtained a specimen on St. Thomas, USVI, but at the time the specimen was not identified to species. The St. Thomas specimen was housed at the U. S. National Museum of Natural History (NMNH), Washington, DC, among unidentified specimens until Dr. Charles O. Handley, Jr. recognized it as *S. rufum* (Hall and Tamsitt 1968). Three living individuals captured in 1957 on St. John, USVI (Hall and Bee 1960), confirmed the contemporary existence of this species. These three specimens were deemed indistinguishable from the holotype and they established St. John as the type locality (Hall

and Bee 1960). Differences in cranial and external measurements led Hall and Tamsitt (1968) to classify specimens from Puerto Rico as a new subspecies, *S. rufum darioi*, and Choate and Birney (1968) characterized fossil remains from Puerto Rico as a separate subspecies, *S. r. anthonyi*. Since confirmation of the existence of this species (Hall and Bee 1960), numerous authors have captured these bats on Puerto Rico and various aspects of its natural history and biology are slowly being revealed (e.g., Genoways and Baker 1972; Scogin 1982; Willig and Bauman 1984; Willig and Gannon 1991; Gannon and Willig 1992). We describe a post-lactating, pregnant female specimen of *S. rufum* captured on St. Croix, USVI (Fig. 2) and compare its external and skull measurements to those from female *S. rufum* from Puerto Rico.

## MATERIALS AND METHODS

On the evening of 10 June 2004, we set three mist nets (38 mesh; Avinet, Dryden, NY) near the Creque Reservoir, in the West End Quarter, Frederiksted District, St. Croix, USVI. Creque Ghut, paralleled by Creque Dam Road, winds up a long, steeply sloped ghut through secondary growth rain forest (Beard 1949). This semi-evergreen rainforest covers the northwestern third of St. Croix and receives ap-

proximately 110-140 cm of rain a year. Creque Ghut is one of a very few locations on St. Croix with permanent running water (in the "swimming hole" area), although most of its length is intermittent stream. The over-story is dominated by kapok (*Ceiba pentandra*), sandbox (*Hura crepitans*), and mango (*Mangifera indica*). The under-story is dominated by tan-tan (wild tamarind, *Leucaena leucocephala*). One mist net was



Figure 2. Photograph of live female *Stenoderma rufum* captured on St. Croix, 10 June 2004.

set along the length of the top of reservoir dam. A second mist net was set perpendicular to the dam, parallel to and between the reservoir and Creque Dam Road. The third net was set approximately 50 m east (upstream) of the reservoir, in the ghat leading to the reservoir, and at a location known as the “swimming hole.” The locality is identified as: St. Croix; Frederiksted District; Northside A; Creque Reservoir; 0.25 km south, 0.1 km east Frenchman Hill; 17°44'45"N, 64°52'32"W. Elevation of the netting site ranged from about 65 m (dam) to 100 m (swimming hole).

Mist nets were open from approximately 1845 to 2230 hr. Netted bats were held until all nets were dismantled to reduce their stress and to prevent recapture. After all nets were closed and secured, the bats were weighed (g), the forearm measured (mm) as the distance from the olecranon process to the tip of the carpals with the wing in a retracted position, and each bat was examined for ectoparasites, age, reproductive condition, and health status before being either released or held for further processing. Bats held for further processing

were fixed in formalin for a minimum of 48 hrs at 4–10°C before being transferred to 70% ethanol and transported back to The University of Scranton. These became voucher specimens deposited at the Museum of Texas Tech University, Lubbock, Texas. The captured *S. rufum* was assigned catalog number TTU-M104503, and the skull was cleaned (dermestid beetles) and subsequently measured. Measurements were taken following Hall (1946), except the greatest length of the skull included the incisors. The single specimen of *S. rufum* captured on St. Thomas in 1943 by Harry A. Beatty was not previously measured. This specimen is a parous female, non-reproductive at capture, stored in alcohol at the National Museum of Natural History (NMNH) as 271210, and no data or measurements were reported. At our request, the skull was extracted and prepared and we report cranial and external measurements. Our measurements of the St. Croix and St. Thomas *S. rufum* were compared to other measurements of female *S. rufum* from Puerto Rico and St. John that were currently available from literature.

## RESULTS

The weather at the netting site on St. Croix, 10 June 2004, was partly cloudy with occasional showers, temperature was 27°C and humidity was 93% (Kestrel 3000 Pocket Weather Meter, Nielsen Kellerman, Chester, PA) at 1830 hr prior to a rain shower. After a 5 min down-pour, while opening nets at 1830-1835 hr, humidity increased to 99-100% and remained elevated for the remainder of our net sets. At 2230 hr, temperature was 25.5°C. From ca. 1830 to 2230 hr we captured 13 *Artibeus jamaicensis*, 2 *Molossus molossus*, and 1 *Stenoderma rufum*. No bats were captured after 2130 hr. The *S. rufum* was captured in the second net parallel to and between the reservoir and the road, elevation 68 m. This bat was flying from the road to the reservoir.

The captured *Stenoderma rufum* was post-lactating (fur worn around obvious mammary gland nipples) and pregnant. The coloration of this St. Croix *Stenoderma* was tan to light brown, with a slight rust color to hairs of dorsum of forelimbs, hindlimbs, and uropatagium, whereas the undersides appeared to contain more grayish than tan or brownish color and no hint of reddish coloration. In a hand-written note submitted with the St. Thomas specimen to NMNH, Harry A. Beatty described color "in the unsoaked condition is brown." The alcohol soaked specimen presently appears light brown to tan, but the color may have been affected by leaching of pigment while stored. For the St. Croix specimen, there were two, bilaterally symmetric, white spots, one located where the wing joins the body and another longer, crescent-shaped white spot directed anteriorly and ventrally to each ear. There was also a ring of white fur surrounding the mouth (Fig. 2). These white areas were best viewed from lateral and ventral views.

The greatest length of mandible and height of coronoid process (in mm), respectively, of the St. Croix (13.49, 7.74) and St. Thomas (14.25, 7.47) specimens are within ranges for the species (Table 1). These values are comparable to values for St. John and contemporary Puerto Rican specimens, but less than fossil Puerto Rican specimens. Fossil lower jaws of five female (presumed) *S. r. anthonyi* from sub-Recent deposit in Cueva de Clara, Puerto Rico, measured in

mm (mean + SD): greatest length of mandible, 14.64 ± 0.15; height of coronoid process 7.96 ± 0.26 (Choate and Birney 1968). These fossil mandibular lengths were greater than those of contemporary Puerto Rican, St. Croix, St. John, and St. Thomas specimens, whereas the height of the coronoid process was larger from fossils than from St. Croix, St. John, and St. Thomas specimens but comparable to *S. r. darioi* (7.90 ± 0.04) from contemporary Puerto Rican specimens.

The total length of the body and the length of the forearm (67.0, 50.21 mm, respectively) of the female St. Croix *Stenoderma* are similar to the average value found for Puerto Rican females (67.8 mm, 49.7 mm) and larger than values for the female St. John specimen (65.0 mm; 47.0 mm). No total body length was available for the St. Thomas specimen but forearm length (50.18 mm) was similar to the St. Croix specimen. The length of the foot of the St. Croix specimen (13 mm) is considerably smaller than the length of the foot from the St. John (16 mm) and St. Thomas (15 mm) specimens, but not different from the average value for female Puerto Rican specimens (13.8 ± 0.37 mm). There was no difference in the length of the ear from St. Croix, St. John, and St. Thomas specimens (18 mm) and the average value from Puerto Rican specimens (17.8 ± 0.20 mm).

For eight characters (total length, length of ear, length of forearm, greatest length of skull, condylo-basal length, mastoid breadth, zygomatic breadth, and maxillary tooth row), measurements (Table 1) from the St. Croix specimen were greater than values from the St. John specimen, but were comparable to St. Thomas and Puerto Rican specimen values. Five characters (postorbital constriction, breadth across upper molar 2, greatest length of mandible, depth of skull, and height of coronoid process) were similar in values between St. Croix, St. John, St. Thomas, and Puerto Rican specimens. The breadth of the braincase was similar in St. Croix and St. Thomas specimens, but greater than the St. John and Puerto Rican specimens. The basal length of the skull was similar in St. Croix and St. Thomas specimens but greater than the St. John specimen (no comparable measurements available for Puerto Rican specimens).

Table 1. Measurements (mm) of *Stenoderma rufum* from St. Croix, USVI (TTU-M104503), compared to female specimens from USVI and Puerto Rico. The St. Croix and St. Thomas specimen values have never been reported previously while all other values are derived from literature cited.

Measurement	St. John		St. Thomas		St. Croix		Puerto Rico	
	<i>Stenoderma r. rufum</i>		<i>S. r. rufum</i>		TTU-M104503		<i>S. r. darwini</i>	
	female	female	female	female	female	El Yunque <sup>c</sup> mean ± SD females	El Yunque <sup>b</sup> mean ± SE (n females)	<i>S. r. anthonyi</i> mean ± SD females
Total length	65.00	65.00	67.00				67.80 ± 0.66 (5)	
Length of hind foot	16.00	16.00	15		13.00		13.80 ± 0.37 (5)	
Length of ear	18.00	18.00	18		18.00		17.80 ± 0.20 (5)	
Length of forearm	47.00	47.30	50.18		50.21		49.70 ± 0.36 (5)	
Greatest length of skull	22.00	22.10	23.29		22.8	22.83 ± 0.35	22.90 ± 0.10 (7)	
Basal length	16.10	17.63	17.21					
Basilar length	15.50		16.75		16.96			
Condylbasal length	18.70		19.97*		20.87	19.46 ± 0.31		
Condyllocanine length			20.05*		21.09			
Breadth of braincase	5.50	10.60	11.96		11.78	10.81 ± 0.22	10.80 ± 0.11 (7)	
Postorbital constriction		5.70	6.09		5.99	5.62 ± 0.12	5.70 ± 0.06 (7)	
Rostral breadth	12.50	12.50	9.1		9.74	9.7 ± 0.20	12.70 ± 0.14 (7)	
Mastoid breadth	14.90	14.70	13.01		12.89	12.54 ± 0.29		
Width of zygomatic arch			7.54*		7.54*	7.47 ± 0.20		
Zygomatic breadth			15.75		15.38	15.2 ± 0.28	15.40 ± 0.08 (7)	
Incisive foramen length			1.16*		1.02*			
Palatal length					4.47	4.16		
Maxillary tooth row	6.80	6.80	7.14*		7.09*	7.03 ± 0.10	7.20 ± 0.07 (7)	
Width of upper molar 2			2.43*		2.30*	2.22 ± 0.13		
Breadth across upper molars, M2		9.60	9.95		9.69	9.68 ± 0.17	10.00 ± 0.06 (7)	
Breadth across upper canines					6.17	6.07	5.91 ± 0.14	
Length of upper molariform tooth row					6.11*	6.05*	5.92 ± 0.18	
Greatest length of mandible	13.70	13.50	14.25*		13.49*	12.61 ± 0.21	13.90 ± 0.06 (7)	14.64 ± 0.15 <sup>d</sup>
Length of mandibular tooth row		12.50	7.31*		7.07*	7.12 ± 0.15		
Depth of skull			11.99		12.32	12.12 ± 0.28	12.30 ± 0.11 (7)	
Length of bullae			3.09*		2.66*	2.64 ± 0.18		
Width of bullae			2.82*		3.14*	3.35 ± 0.19		
Width of maxilla			4.6*		4.28*	3.83 ± 0.15		
Height of coronoid process			7.70		7.47*	7.74*	7.90 ± 0.04 (7)	7.96 ± 0.26 <sup>d</sup>
Least interorbital breadth			3.48*		3.54			

\* average of bilateral measurements

<sup>a</sup> Hall and Bee 1960

<sup>b</sup> Jones et al. 1970 reported values as means ± standard error (SE).

<sup>c</sup> Gannon et al. 1992 reported values as means ± standard deviation (SD), n = 58.

<sup>d</sup> Choate and Birney 1968; values derived from Fig. 5, n = 5.

## DISCUSSION

The finding of *Stenoderma rufum* on St. Croix has increased the known geographic range for this species and it may be more extensive than that currently known. The genera *Stenoderma*, *Ardops*, *Phyllops*, and *Ariteus*, all of which have a white shoulder spot and shortened rostrum, are parapatric genera that form the Antillean endemic subtribe *Stenodermatina* believed to have evolved from a single, ancestral invader, that subsequently radiated and diversified on West Indian islands before populating the mainland (Baker and Genoways 1978; Baker et al. 2003; Genoways et al. 2005). Because the *S. rufum* we found was pregnant and post-lactating, a reproductive population has been found off the Puerto Rican bank for the first time. Finding a pregnant female in June was not surprising because this species is asynchronously polyestrous and pregnancy could occur any time of year (Gannon and Willig 1992).

The significance of this record is that it is the first for the genus *Stenoderma* beyond the Puerto Rican bank. The Virgin Islands form two quite distinct geographical units. Vieques, Culebra, St. Thomas, St. John, Tortola, Virgin Gorda, Anegada, and associated smaller cays, collectively are known as the Northern Virgin Islands, whereas St. Croix and its smaller cays form the Southern Virgin Islands (Fig. 1). The Northern Virgin Islands are on the Puerto Rican bank, which formed a land extension of Puerto Rico until about 10,000 years ago and is known as the Virgin Island Platform (Heatwole and Mackenzie 1967). Southeast of the Virgin Island Platform, St. Croix is a pinnacle of an east-trending submarine ridge, the St. Croix Platform. St. Croix and its associated cays, approximately 68 km south of St. John and St. Thomas and 101 km southeast of Puerto Rico, are flanked by the Caribbean Sea Basin (specifically, the 4,500 m deep Virgin Island Basin) and to the southeast by Aves Ridge. The tectonic complex of St. Croix has no evident equivalent on islands of the northeastern Caribbean (Speed 1989). Volcanogenic sediments of comparable age on Puerto Rico and the northern Virgin Islands have not had similar depositional, deformational, or metamorphic histories as those of St. Croix (Speed 1989; Speed and Joyce 1989; Speed and Larue 1991; Larue 1994). Puerto Rico and the northern Virgin Islands emerged from submarine volcanic mountains near the Juras-

sic-Cretaceous boundary and separated by rising sea levels and tectonic contractions (Larue 1994), whereas St. Croix has been emergent for the last 3-4 ma only (Speed 1989; McLaughlin et al. 1995). St. Croix's distinct geological origin and independence from the northern Virgin Islands indicates that bat populations most likely arrived by over water dispersals to St. Croix from adjacent islands, similar to that espoused by Hedges (1996), and not by vicariance (Rosen 1975) or by a combination of dispersal and vicariance (Iturralde-Vinent and MacPhee 1999).

The location of the type locality is unknown, but the name *Stenoderma rufum* was restricted to specimens from St. John because they are indistinguishable from the holotype in pallor of pelage (Hall and Bee 1960). The dorsal coloration of *S. r. rufum* from St. John are described as tan to buckthorn brown with a reddish hue and underparts that are paler and less reddish and indistinguishable from the holotype (Hall and Bee 1960). Color of the dorsum of Puerto Rican *S. r. darioi* varies from tan to dark chocolate brown or Dresden brown, whereas color of the ventrum is paler (Jones et al. 1971; Genoways and Baker 1972). The dorsum of the St. Thomas specimen was described as "brown" and its current alcohol soaked condition appears light brown to tan. The dorsum of the St. Croix specimen was light brown to tan, not chocolate brown, lighter than buckthorn brown, and appeared as a variant similar to St. John specimens; therefore, all Virgin Island specimens are similar in coloration and lighter in color than Puerto Rican specimens.

The habitats of the two subspecies of *Stenoderma rufum* differ in that *S. r. rufum* previously has been found in dry arborescent vegetation on St. John and *S. r. darioi* typically has been found in dense rain forest in Puerto Rico (Hall and Tamsitt 1968). The St. Croix *S. rufum* was found in secondary rain forest, whereas the St. Thomas specimen was captured along a "streamway" (handwritten notes of Harry A. Beatty) in habitat that is dry scrub and arborescent vegetation.

The cranium of the St. Croix specimen is larger than the crania of females from St. John but comparable to the cranium of the female specimen from St.

Thomas and female specimens from Puerto Rico. Based on available measures for female *S. rufum*, the overall size of external characters and cranial characters of the St. Croix and St. Thomas specimens are more similar to female Puerto Rican *S. r. darioi* than to St. John *S. r. rufum*. For example, the crania of Puerto Rican specimens are longer than those from St. John and the length of the crania of the St. Croix and St. Thomas specimens are longer than the cranium of the St. John female but comparable in length to those of females from Puerto Rico. Size of entire individual, external characters, size of cranium, and shape of skull do not differ radically between the two subspecies, but pelage color is consistently different (Hall and Tamsitt 1968). The St. Croix and St. Thomas specimens are both similar in pelage and are consistent with the Virgin Island subspecies *S. r. rufum*. Neither morphological characters nor habitat characteristics clearly align the St. Croix specimen with either subspecies, but pelage is consistent with *S. r. rufum*, and therefore, we tentatively assign the

St. Croix *Stenoderma* to *S. r. rufum*. If secondary sexual dimorphism holds for the St. Croix *Stenoderma*, then males would be expected to be smaller than females, as this was the finding for Puerto Rico (Gannon et al 1992) and for St. John (Jones et al. 1971) specimens.

It had been predicted that St. Croix would lack some of the faunal elements present on the other Virgin Islands and absent in the Lesser Antilles and for bats, this was true only for *Stenoderma rufum* (Koopman 1975). St. Croix can now claim to have the same bat fauna as the other Virgin Islands, except for *Tadarida brasiliensis*. The only records of the widespread *T. brasiliensis* from the Virgin Islands are netted specimens from St. John (Hall and Bee 1960), and there are no data on roosting sites in the Virgin Islands for this species. *S. rufum* is the only bat species on the Virgin Islands not found in the Lesser Antilles.

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#### LITERATURE CITED

- Allen, G. M. 1911. Mammals of the West Indies. Bulletin of the Museum of Comparative Zoology at Harvard University 54:175-263.
- Anthony, H. E. 1918. The indigenous land mammals of Porto Rico, living and extinct. Memoirs of the American Museum of Natural History 2:331-345.
- Anthony, H. E. 1925. Scientific survey of Porto Rico and the Virgin Islands. Part I. Mammals of Porto Rico, living and extinct—Chiroptera and Insectivora. New York Academy of Sciences 9:1-96.
- Baker, R. J., and H. H. Genoways. 1978. Zoogeography of Antillean bats. Pp. 53-97 in Zoogeography in the Caribbean (F. B. Gill, ed.). Special Publication, Academy of Natural Sciences of Philadelphia 13:1-128 + iii.
- Baker, R. J., S. R. Hooper, C. A. Porter, and Ronald A. Van Den Bussche. 2003. Diversification among New World leaf-nosed bats: an evolutionary hypothesis and classification inferred from digenomic congruence of DNA sequence. Occasional Papers of the Museum, Texas Tech University 230:1-32.
- Beard, J. S. 1949. The natural vegetation of the windward and leeward islands. Oxford University Press, London, England.
- Choate, J. R., and E. C. Birney. 1968. Sub-recent insectivore and chiroptera from Puerto Rico, with the description of a new bat of the genus *Stenoderma*. Journal of Mammalogy 49:400-412.

- Demarest, A. G. 1820. Mammalogie, ou description des espèces de mammifères. Paris 1:1-276.
- Gannon, M. R., and M. R. Willig. 1992. Bat reproduction in the Luquillo Experimental Forest of Puerto Rico. *Southwestern Naturalist* 37:414-419.
- Gannon, M. R., M. R. Willig, and J. K. Jones, Jr. 1992. Morphometric variation, measurement error, and fluctuating asymmetry in the red fig-eating bat (*Stenoderma rufum*). *Texas Journal of Science* 44:389-404.
- Genoways, H. H., and R. J. Baker. 1972. *Stenoderma rufum*. *Mammalian Species* 18:1-4.
- Genoways, H. H., R. J. Baker, J. W. Bickham, and C. J. Phillips. 2005. Bats of Jamaica. *Special Publications, Museum of Texas Tech University* 48:1-155.
- Geoffroy St.-Hilaire, É. 1818. Description des mammifères qui se trouvent en Égypte. Pp. 99-166 in Description de l'Égypte ou recueil des observations et des recherches qui ont été faites en Égypte pendant l'expédition de l'armée Française [1798-1801]: Histoire Naturelle. Paris 2:1-218.
- Hall, E. R. 1946. *Mammals of Nevada*. University of California Press, Berkeley.
- Hall, E. R., and J. W. Bee. 1960. The red fig-eating bat *Stenoderma rufum* Desmarest found alive in the West Indies. *Mammalia* 24:67-75.
- Hall, E. R., and J. R. Tamsitt. 1968. A new subspecies of the red fig-eating bat from Puerto Rico. *Life Science Occasional Papers, Royal Ontario Museum* 11:1-5.
- Heatwole, H., and F. Mackenzie. 1967. Herpetogeography of Puerto Rico. IV. Paleogeography, faunal similarity and endemism. *Evolution* 21:429-438.
- Hedges, S. B. 1996. Historical biogeography of West Indian vertebrates. *Annual Review of Ecology and Systematics* 27:163-196.
- Iturralde-Vinent, M., and R. D. E. MacPhee. 1999. Paleogeography of the Caribbean region: implications for Cenozoic biogeography. *Bulletin of the American Museum of Natural History* 238:1-95.
- Jones, J. K., Jr., H. H. Genoways, and R. J. Baker. 1971. Morphological variation in *Stenoderma rufum*. *Journal of Mammalogy* 52:244-247.
- Koopman, K. F. 1975. Bats of the Virgin Islands in relation to those of the Greater and Lesser Antilles. *American Museum Novitates* 2581:1-7.
- Larue, D. K. 1994. Puerto Rico and the Virgin Islands. Pp. 151-165 in *Caribbean geology. An Introduction* (S. K. Donovan and T. A. Jackson, eds.). The University of the West Indies Publishers' Association, Kingston, Jamaica.
- McLaughlin, P. P., Jr., L. P. Gill, and W. A. van den Bold. 1995. Biostratigraphy, paleoenvironments and stratigraphic evolution of the Neogene of St. Croix, U. S. Virgin Islands. *Micropaleontology* 41:293-320.
- Peters, W. 1869. Bemerkungen über neue order weniger bekannte Flederthiere, besonders des Pariser Museums. Pp. 391-408 in *Monatsberichte der Königlichen Preussische Akademie des Wissenschaften zu Berlin. Königlichen Akademie des Wissenschaften, Berlin*.
- Peters, W. 1876. Las über *Stenoderma* Geoffroy und eine damit verwandte neue Flederthier-Gattung, *Peltorhinus*. Pp. 429-434 in *Monatsberichte der Königlichen Preussische Akademie des Wissenschaften zu Berlin. Königlichen Akademie des Wissenschaften, Berlin*.
- Rosen, D. E. 1975. A vicariance model of Caribbean biogeography. *Systematic Zoology* 24:431-464.
- Scogin, R. 1982. Dietary observations on the red, fig-eating bat (*Stenoderma rufum*) in Puerto Rico. *Alsio* 10:259-261.
- Speed, R. C. 1989. Tectonic evolution of St. Croix: implications for tectonics of the northeastern Caribbean. Pp. 9-22 in *Terrestrial and marine geology of St. Croix, U. S. Virgin Islands* (D. K. Hubbard, ed.). *Special Publication, West Indies Laboratory, St. Croix, USVI* 8:9-22.
- Speed, R. C., and J. Joyce. 1989. Depositional and structural evolution of Cretaceous strata, St. Croix. Pp. 23-36 in *Terrestrial and marine geology of St. Croix, U. S. Virgin Islands* (D. K. Hubbard, ed.). *Special Publication, West Indies Laboratory, St. Croix, USVI* 8:23-36.
- Speed, R. C., and D. K. Larue. 1991. Extension and trans-tension in the plate boundary zone of northeastern Caribbean. *Geophysical Research Letters* 18:573-576.
- Timm, R. M., and H. H. Genoways. 2003. West Indian mammals from the Albert Schwartz Collection: biological and historical information. *Scientific Papers, Natural History Museum, The University of Kansas* 29:1-47.

Willig, M. R., and A. Bauman. 1984. Notes on bats from the Luquillo Mountains of Puerto Rico. Center for Energy and Environmental Research, University of Puerto Rico. CEER-T-194:1-12.

Willig, M. R., and M. R. Gannon. 1991. Mammalian ecology in a Puerto Rican Rain Forest. Pp. 400-431 in A tropical food web (R. B. Waide and D. P. Reagan, eds.). University of Chicago Press, Chicago, Illinois.

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